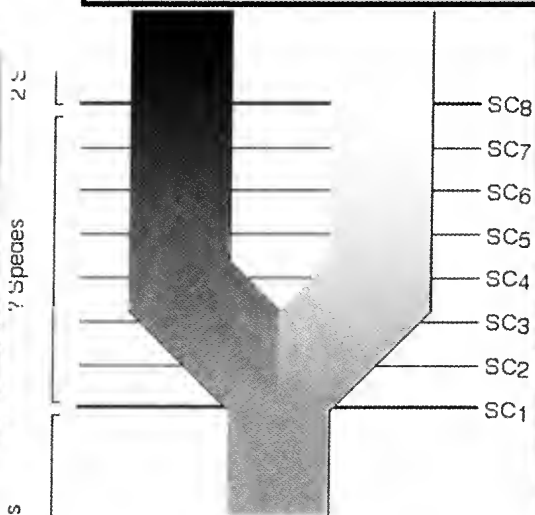


Biodiversity and Taxonomy

Arranged and edited by
Nina G. Jablonski and Michael T. Ghiselin



Observation
(specimens, characters)

Reality
(phylogenetic)

California Academy of Sciences
and the
Pacific Division of the American Association
for the Advancement of Science

Conceptualization of reality

current land area

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Proceedings of the Symposia

**BIODIVERSITY
PAST, PRESENT, AND FUTURE
and
THE FUTURE OF TAXONOMY**

**held on the occasion of the 150th Anniversary of the
California Academy of Sciences**

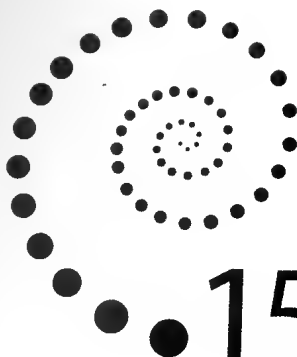
June 17–18, 2003

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**Presented on the campus of San Francisco State University
San Francisco, California**



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Editors' Note

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**Introduction to the Combined
Biodiversity and Taxonomy Symposium Supplement
Biodiversity and Taxonomy for the 21st Century**

Nina G. Jablonski

The 150th anniversary of the California Academy of Sciences was celebrated in 2003 by a variety of activities, including a retrospective exhibit on Academy history and three scholarly symposia. This supplement to the Proceedings of the California Academy of Sciences contains the fully edited and peer-reviewed proceedings of two of those symposia, "Biodiversity: Past, Present, and Future" and "The Future of Taxonomy," which were held in June 2003 in conjunction with the annual meeting of the Pacific Division of the American Association for the Advancement of Science in San Francisco.

Over the years, the enterprise of systematic biology has come to dominate the scientific activities of the Academy. As the foundation discipline of biology, systematic biology embraces the study of the classification and evolutionary relationships of all living things. The focal points of the symposia represented here — biodiversity studies "What is out there?" and taxonomy "What is it called?" — constitute two of the major disciplines within systematic biology and are intellectually co-dependent. Studying the diversity of life on Earth clearly requires a robust and usable system for naming and classifying organisms.

The last decade has witnessed crises in both disciplines, and it is from these crises that the current volume has sprung. On the side of biodiversity studies, the crises have been born of the urgency to study the Earth's increasingly threatened biota in the face of a shortage of resources and the will to do so. On the side of taxonomy, the field has been beset by intellectual struggles within the discipline — largely over the future utility of the Linnaean hierarchy and system of naming — and attacks from outside of the discipline, focused on the cumbersome nature of the taxonomic enterprise and the difficulty of accessing taxonomic information.

Readers of this volume will discover that the papers herein address these crises head on, with an honest airing of diverse perspectives and potential solutions. Because systematic biologists have been quick to embrace technological breakthroughs in molecular biology, developmental biology, informatics, and computer sciences, a fundamental optimism about the future emerges from the depths of these papers. Systematic biology is an information-rich and information-dependent science, and our abilities to address basic and applied problems in studies of biodiversity and taxonomy increasingly rely on our abilities to organize, marshal, and disseminate information efficiently and authoritatively. The biggest challenge facing students of biodiversity and taxonomy is not intellectual inertia, but the need to build and maintain a critical mass of practitioners. Maintenance of a healthy community of scientists contributing to systematic biology is not just desirable for society, it is essential, especially as we wrestle with fundamental questions of how much biodiversity we need to know about and how much we need to preserve. In this connection, natural history museums such as the California Academy of Sciences will play progressively important roles in igniting the interest of future scientists and citizens, providing training in systematic biology, main-

taining physical collections of our planet's biotic diversity, and promulgating information on this diversity to audiences throughout the world.

ACKNOWLEDGMENTS

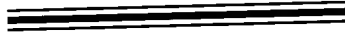
The papers in this volume were originally presented in the symposia, "The Future of Taxonomy," and "Biodiversity: Past, Present, and Future," two of three symposia¹ that were organized to mark the 150th anniversary of the California Academy of Sciences in 2003. The three symposia were co-sponsored by the Pacific Division of the American Association for the Advancement of Science (AAAS-PD) and were presented during the annual meeting of the AAAS-PD that was held on the campus of San Francisco State University (SFSU) in June 2004. The symposia were made possible by the financial support of the California Academy of Sciences, and specifically by funds mobilized by the Academy's inspired and dedicated provost, Dr. Terrence Gosliner. Logistical support provided by the executive officer of the AAAS-PD, Dr. Roger Christianson, and his staff, and by the conference staff of SFSU was critical to making these symposia a success. The papers in this volume were reviewed by dozens of colleagues from around the world who took time from their busy schedules to provide thoughtful and constructive comments to authors. To all of these people and organizations, I owe a large debt of gratitude. I am hopeful that these contributions will provide inspiration and information for much-needed research and public outreach in these vital, but mostly ignored, realms of knowledge.

¹ The papers presented at the third symposium, "Museums and Other Institutions of Natural History: Past, Present, and Future," were published in the *Proceedings of the California Academy of Sciences*, ser. 4, volume 55, supplement I on 18 October 2004.

BIODIVERSITY

**A Symposium
held on the occasion of the 150th Anniversary of the
California Academy of Sciences
June 17–18, 2003**

**and sponsored by
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for the Advancement of Science**



**Presented on the campus of San Francisco State University
San Francisco, California**

Arranged and edited by

Nina G. Jablonski
California Academy of Sciences

Exploring Biodiversity: Past, Present, and Future

Nina G. Jablonski

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The field of biodiversity studies now embraces the activities of many disciplines, including paleobiology, systematics, ecology, and conservation biology. The breadth of the basic scientific research in this field is well represented by the collection of papers in this special issue. These studies present new data, syntheses, and opinions on how we can best document and preserve biodiversity given the limitations of human behavior and resources. All the contained studies emphasize the importance of interdisciplinary collaboration, integration of data from diverse sources, and collective scientific and social action.

Since the neologism ‘biodiversity’ was coined by E.O. Wilson in 1986 as a catchy replacement for ‘biological diversity’, the word has achieved broad currency in the professional and popular scientific and environmental literature. In the last twenty years, worries over the hastening pace of extinctions, the ramifications of global warming, and the ecological and economic impacts of invasive species have spawned unprecedented levels of awareness and concern for the Earth’s biota. What began as a single word — biodiversity — is now an entire field of study, which brings together paleobiologists, systematists, ecologists, climatologists, biogeographers, geneticists, and conservation biologists, just to name a few. The idea of having the California Academy of Sciences host a symposium with a focus on the dynamic and multidisciplinary theme of “Biodiversity: Past, Present, and Future” emerged early in the course of planning for the 150th anniversary of the Academy, which was celebrated throughout 2003. Thanks to the generosity of the Pacific Division of the American Association for the Advancement of Sciences, the two-day symposium was co-hosted by the Division and the Academy, and held on the campus of San Francisco State University on June 16–17, 2003 as part of the Pacific Division’s annual meeting. The symposium was well attended and enthusiastically received. Those who were able to attend most or all of the papers were amply rewarded with papers ranging from the data-rich and synthetic to the innovative and provocative. Some exceptional papers triumphed in all of these areas.

The papers in this volume represent a good sample of the basic research underpinning the emerging field of biodiversity sciences today, and celebrate the breadth of inquiry now being explored by scientists at the California Academy of Sciences and many other institutions. Whereas many conferences and volumes dedicated to biodiversity have focused exclusively on living biotas, this collection comprises papers exploring biodiversity in the past, present, and future, and provides the reader with vivid insights as to how these studies can mutually inform one another.

The questions broached in these papers are dauntingly big. How do we ascertain and measure biodiversity? How has biodiversity changed through time? To what extent is loss of biodiversity being hastened by recent human activities? How can we realistically approach the societal issues raised by biodiversity and conservation studies without losing direction and heart? The first four

papers in this collection represent dramatically different types of investigations of past biodiversity. Geerat Vermeij breaks new ground by probing the origins of the fundamental patterns of species diversity. He specifically examines the roles played by global temperature in creating the gradients of species diversity that we observe in today, and by competition for local limiting resources in promoting functional differentiation and specialization of species. Douglas Erwin seeks new answers to questions surrounding the origins of the Cambrian metazoan radiation by integrating data from paleoecology and developmental biology. William DiMichele, Robert Gastaldo and Hermann Pfefferkorn provide innovative insights into the rules governing the assembly of ecological communities through detailed examination of Paleozoic tropical ecosystems. Their focus on the role of vascular plants in creating new niches for other organisms in early terrestrial ecosystems is particularly enlightening. Patterns of species diversity and species association through time are also the subject of the paper by Anthony Barnosky and Alan Shabel. These authors explore these phenomena through an examination of mammalian species diversity from a single site in North America in both Pleistocene and historic times, and conclude that patterns of species association and community structure are remarkably robust, even in the face of major environmental changes.

Five papers in this collection focus on biodiversity of modern biotas. The first of these, by Daniel Dykhuizen, will startle most biologists dealing with multicellular organisms by bringing forth a definition of bacterial species based on DNA hybridization that relegates metazoan species to the role of genetically depauperate bystanders in evolution. Based on his conservative definition of bacterial species, Dykhuizen estimates that the Earth is home to at least one billion species of bacteria. Questions surrounding the actual numbers of metazoan species in terrestrial ecosystems and the factors influencing species diversity are explored for two families of beetles by Terry Erwin, María Pimentia, Oscar Murillo, and Valeria Aschero. The results of their study challenge widely held assumptions concerning the composition of assemblages of herbivore and predator species in tropical ecosystems, and provoke re-examination of the methods we use to ascertain and preserve species in such ecosystems. Insect biodiversity and its ascertainment are also the subjects of the paper by Brian Fisher, in which he describes his ambitious and large-scale project for inventorying and reporting the ant fauna of Madagascar. He convincingly demonstrates that it is possible to undertake and broadcast a comprehensive inventory of a speciose biota, but that the costs in terms of money and human effort are significant. This contribution and that by T. Erwin and colleagues provide rare insights into the real costs and benefits of biodiversity analyses, and should provide important basic data for conservation strategists and policy planners. The issues involved with the conduct of multi-taxon surveys in the populous and biodiverse country of Vietnam are broached by Eleanor Sterling and Martha Hurley. Their study highlights the challenges faced by biodiversity scientists working in threatened habitats, and reinforces the oft-forgotten points that wide-scale surveys can yield discoveries of new metazoan species and range extensions of familiar species in even fairly well-studied terrestrial habitats. Their exemplary study also emphasizes the importance of teams employing comparable methodologies conducting biological inventories in countries or regions that span a wide range of latitudes or ecological zones. Julia Berger, in her paper reviewing the work of the All Species Foundation (ALL), illustrates how the goals of organizations like the ALL must adapt to the changing intellectual and financial environments in which they operate. The original goal of the ALL — the ascertainment of all remaining species on Earth in 25 years — was scaled down in 2002 to the more modest, but more realistic and important, goal of developing tools and technologies to facilitate the creation and dissemination of taxonomic information.

The final three papers in this collection provide varied and provocative food for thought on the status and prospects of biodiversity. Michael McKinney begins this trilogy by examining the

impact of humans on patterns of biodiversity. His troubling but accurate description of a 'New Pangea' emphasizes the human penchant for dispersing species, creating new and unlikely mixtures of species, and fragmenting habitats. His is not the usual treatment of invasive species at a local level, but a clarion call to scientists and policy makers to examine the costs of human behavior at a global scale. In the following paper, Paul Ehrlich challenges systematic biologists to face the problems of biodiversity decline by coming up with more efficient methods for sampling the world's biota and promulgating the results of their investigations. Far from advocating ascertainment of all species, he supports the development of selective inventories, especially of metazoan biotas that are already reasonably well known, and the concerted cooperation of systematists and ecologists in disseminating relevant information on biodiversity to the scientific community and makers of public policy. The last paper in this volume, by Peter Raven, calls attention to the problems of human impacts on the Earth's biota from a different perspective. Humans are a destructive and manipulative species, but they also vary greatly from one region and economic sphere to the other in their tendencies. They are also the only species to be fully aware of the local and global impacts of their activities. Raven stresses that awareness at this point is far from sufficient, however, and that we must apply our faculties and considerable creativity to reining in our species' ecologically malignant tendencies for overconsumption.

Four important and overarching messages emerged from the symposium and from the papers in this collection. The first is that an understanding of biodiversity at the local, regional, or global levels is possible only if individual scientists are more explicitly integrative and interdisciplinary in their work. This may involve investigation of literature in cognate fields, or actual discussion and collaboration with scientists in these fields. Systematics and ecology - the very foundations of biodiversity studies - must put aside their minor doctrinal differences and rise to the challenges now facing their science and their planet. The second is that scientists engaged in research in any one of the disciplines supporting biodiversity science must make an effort to see that the results of their work are disseminated beyond the typically very small academic circles in which most of navigate. This is especially true of scientists who carry out surveys or studies with implications at any level for public policy. The third is that we must get a lot better at advertising the importance and relevance of what we do to the general public. The discovery of biodiversity should, it has been argued, garner as much public attention and financial support as space exploration because it is just as exciting. This is demonstrably not the case, however. Individual scientists really can make a difference here, by reaching out in whatever ways they can to communicate the marvels of life of Earth to others. The fourth and final message is that those of us who engage in the scientific study of biodiversity are also citizens of the Earth. Our social responsibilities should be informed by our research, and activism at some level should become as much a part of our lives as fieldwork and the writing of papers.

Taken together, the papers in this collection inspire awe — at the vast amounts we know and don't know — and, most importantly, action.

From Phenomenology to First Principles: Toward a Theory of Diversity

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Diversity is a phenomenon that biologists typically associate with species, but in fact it characterizes all economic systems in which there is competition for locally limited resources. Patterns in species diversity — the equatorward increase in species number, the tendency for larger areas to support greater numbers of species, the association between high species richness and sexual selection, and a general increase in diversity through time, among others — are accounted for by two fundamental principles. First, the potential range of available phenotypes increases from conditions of low temperature, near the freezing point of water, to conditions where tropical climates prevail (30 to 40°C), because interactions ranging from the intermolecular to those among species speed up as temperature rises. Diversity also tends to increase from systems with low availability, predictability, and productivity of resources to those in which resources are plentiful, reliably available, yet still subject to local competition. Second, and more important, competition for locally limiting resources promotes division of labor and therefore functional differentiation and specialization. Levels of competition rise and evolutionary responses to competition proceed further in larger economic systems, where many phenotypic options are energetically available. Moreover, the number of resources for which economic entities compete also increases as economies expand and as rates of supply of those resources become increasingly controlled and enhanced by the entities comprising the system. In other words, competition creates positive feedbacks between potential and realized diversity. High diversity in an economic context thus arises when potential differences in performance — success in competition in its broadest sense — are large and when the stakes for survival and reproduction (the benefits of success versus the costs of failure) are high.

To many scientists, there is something seductively attractive about a concept that is at once abstract — devoid of the messy details of reality — and quantifiable. Such a concept is diversity, an expression of variety that has been widely embraced by ecologists, conservationists, paleontologists, sociologists, and even politicians. Perhaps because diversity is an abstract epiphenomenon, a more or less context-independent property of groups not possessed by any single member of that group, its scientific study has very largely been phenomenological, or descriptive. We describe how diversity — the number of species, adaptive types, languages, and so on — varies in space and time at scales ranging from the local community to the global biosphere. Mostly, we think of diversity as a snapshot of variety. We may compare diversity as it varies from place to place or through time, but inferences of process or cause from pattern have generally accomplished little more than to elevate phenomenology to a higher level.

I would point to two primary reasons for our collective failure to understand biological diversity at the species level in a theoretical framework that transcends descriptive phenomenology. First, whereas there is an overwhelming amount of information on the geography of diversity in terrestrial settings — that is, about diversity of creatures on the dry land — studies of diversity in such other environments as the sea, the soil, and the microbial world lag far behind. At the purely descriptive level, therefore, we are missing the richly comparative data that might constrain our musings about the “causes” of diversity as inferred from observed patterns among birds, land plants, mammals, and insects. Second, insufficient attention has been focused on first principles, the laws that describe how variety arises and diminishes. These rules — the economic and physical factors that promote diversity, the categories of calamity that decrease it — are mostly well known; the problem is that they reside in parts of science that are unfamiliar to most scientists who are most directly concerned with diversity. Moreover, the principles governing diversity explicitly introduce context, the very concept that many quantifiers of diversity sought to purge.

I have come to the subject of diversity as both a paleontologist and marine biologist with a taste for understanding the context that creates diversity and that is created by diversity. My aim in this essay is to catalogue briefly the major patterns of biological diversity as revealed by comparative studies in present-day and past oceans and lands, and to identify the principles that account for the phenomenology of diversity.

PATTERNS OF DIVERSITY

Patterns of diversity have been the subject of such a vast literature that I confine myself here to a statement of the main patterns. These are: (1) an increase in species numbers from the poles to the equator, from high to low altitudes on land, and from deep to shallow water in the sea; (2) an increase in diversity with area of habitat, where the number of species rises as area to the 0.2 to 0.3 power, meaning that islands and island-like environments have fewer species than continents or large bodies of water; (3) higher diversity in regions where geographical opportunities for genetic isolation are most numerous, that is, where many barriers exist and where these barriers change frequently in position and permeability; (4) higher diversity in clades (evolutionary units comprising an ancestor and all its descendants) characterized by internal fertilization than in those in which the union of male and female gametes takes place outside the parental bodies; and (e) a general increase in diversity, through time, punctuated briefly by extinction events.

Interested readers should consult Rosenzweig's (1995) comprehensive book for detailed documentation and discussion of these patterns. Here I wish to draw attention to a few potential exceptions, some problems of how to evaluate the relative contribution of factors that have been identified in empirical studies of diversity, and to redirect such studies to variables that more precisely identify the phenomena that cause or promote variety.

Perhaps the best known spatial pattern of diversity is the poles-to-equator increase in species number. Most clades of plants and animals on land and in the sea conform to this latitudinal gradient (for a recent comprehensive review, see Hillebrand 2004). So do human languages and cultures (Pagel and Mace 2004).

There are, however, exceptions. Small zooplankters such as foraminifers and copepods in the pelagic realm reach peak diversities not in the tropics, but at the middle latitudes (McGowan and Walker 1993; Rutherford et al. 1999). According to some interpretations (Rutherford et al. 1999), the water column is more finely and more predictably divided into depth zones at middle than at low latitudes, so that the zooplankton species can specialize to particular depths more in the temperate zones than in either the tropics or the polar regions. The number of zooplankton species is, however, vastly greater than the number of definable depth zones, much as the number of strata in

terrestrial vegetations (three to four layers in temperate and tropical forests; see A.R. Smith 1973; Terborgh 1985) and the number of zones in the intertidal belt do not begin to account for the patterns of diversity among trees or shore animals.

On rocky shores, the diversity of multicellular seaweeds and of the invertebrates that graze them likewise seems to reach a peak at middle northern and southern latitudes (for a review, see Bakus 1969). This pattern does not, however, apply to photosynthesizing animals — corals, gorgonians, some sponges, and even some bivalves — or to herbivorous fishes, which are most diverse in the tropics. The apparent exception of seaweeds and their consumers may disappear if we consider photosynthesizing animals and their consumers instead of seaweeds and their herbivores as the relevant group. My guess is that the diversity of attached multicellular marine primary producers and of their consumers will be found to conform to the typical equatorward increase in species as seen in most other clades and ecological groups.

Latitude is easy to measure, but it is unlikely to be the variable to which diversity or the organisms whose species number is being analyzed respond. Instead, latitude is a proxy for some other variable that is more directly linked to the lives of organisms and to the opportunities and constraints on species formation and loss. There is, for example, a general (if not wholly consistent) rise in temperature, incoming solar radiation, and net primary productivity as one moves from the poles to the equator, that is, with decreasing latitude. Incoming radiation amounts to about 60 W/m² (watts per meter squared) at 80°N, 120 to 125 W/m² at 60°N, and about 200 W/m² at the equator. Poleward of 40° north and south latitude, there is a net loss of radiation. These numbers will vary according to cloudiness and other factors, and may not accurately reflect the ability of organisms to absorb and to use incoming radiation. On land, productivity tends to increase with decreasing latitude, but again there is considerable variation in productivity, higher values occurring in areas of higher rainfall. For this reason, evapo-transpiration is a better proxy for energy in terrestrial ecosystems than incoming radiation (DeAngelis 1992), and is a better predictor of the number of plant and bird species (Wright 1983; Wright et al. 1993).

Temperature, another measure of energy availability, likewise is positively associated with high diversity in both terrestrial and aquatic environments (Vermeij 1978; Rosenzweig 1995; Fraser and Currie 1996; Guégan et al. 1998; Rohde 1999). Both diversity and temperature (mean average, extreme low, and extreme high temperatures) tend to rise toward the equator, but there appear to be important thresholds of temperature that affect diversity regardless of latitude. In the sea, the diversity of bivalves and other bottom-dwelling animals falls sharply south of the transition between the tropics and the temperate zones (Crame 2000, 2002). In Peru, this transition occurs near 5°S, whereas in Australia it is much further south, between 25 and 30°S. Hence, latitudinal gradients are often stepped instead of gradual, and their shape depends very much on where major thermal transitions occur (see also Vermeij 1996). The position of these thermal transitions, in turn, depends on the pattern of oceanic and atmospheric circulation. In Peru, the edge of the biological tropics is determined by the northward extent of the cold Peru Current. In the northwestern Atlantic, the transition zone between the subtropical Carolinian and the cool-temperate Virginian biogeographic regions occurs off North Carolina, and is determined by the interaction between the cold Labrador Current and the warm Gulf Stream. On land, frost eliminates large numbers of warm-adapted species, so the geography of winter frost determines the latitudinal pattern of diversity (Ricklefs and Latham 1993).

Temperature, energy availability, and evapo-transpiration all affect net primary productivity, the rate of production of biomass that is available for consumption by animals and decomposers. In the deep sea below a depth of 500 m, water temperatures are uniformly low (below 4°C), but there is still an equatorward increase in the diversity of bivalves and other bottom-dwelling animals

in the North Atlantic (Culver and Buzas 2000; Rex et al. 2000). In this cold, generally nutrient-poor environment, the best empirical predictor of diversity is net primary productivity in surface waters (Rex 1973, 1976; Rex et al. 1993, 2000). Low diversity at abyssal and greater depths compared to shallower zones on the ocean floor similarly reflect lower availability of usable food. A drop in species numbers toward higher altitudes (Rosenzweig 1995) similarly may be attributable to both lower temperature and lower productivity.

The comparative study of islands, pioneered by MacArthur and Wilson (1967), provides the basis for the generalization that habitat area — or, more generally, the size of ecosystems or communities in which species are embedded — is the most important single factor controlling diversity. Not only does diversity increase with area raised to the 0.2 to 0.3 power, but larger areas can support types of species that smaller areas cannot. In particular, species with low population density but high per-capita demands require large habitats for feeding and are, therefore, excluded from small regions.

Statistical analyses have persuaded many biogeographers that area explains more of the variation in species diversity than do other variables such as temperature, longitude, latitude, or productivity (see e.g., Rosenzweig 1995; Bellwood and Hughes 2001). It is crucial to realize, however, that the contribution a particular variable makes to the range of values of diversity depends entirely on the scale of the analysis. For example, Bellwood and Hughes's (2001) conclusion that area explains more of the regional variation in reef fish and coral diversity than do latitude and longitude arises from the fact that, although a large range of values of area was considered, the range of latitudes was restricted to the 60° of latitude in which coral reefs flourish. With a large range of latitude, or a smaller range of areas, the contribution that each variable makes to diversity would change, with latitude assuming a more prominent role. Estimates of how much variation in a dependent variable is explained by each of several independent "controlling" variables depend on the ranges of the controlling variables. Such estimates must, therefore, be treated with great interpretative caution and should not be taken too seriously. Furthermore, latitude and diversity may be relatively independent of each other in the immediate vicinity of the equator or within the Caribbean basin, but be strongly linked elsewhere. In other words, the nature of the relationship among variables may change from place to place and over time, making any estimates of the relative contribution of a given variable to an epiphenomenon like diversity suspect and unreliable.

Many tectonically active or topographically complex regions harbor large numbers of species, presumably because barriers have formed and shifted frequently. Terrestrial hotspots of diversity include the Himalayas and adjacent parts of China and India, and the Andean region of South America among many others. In the sea, places like the Philippines and the western Pacific generally come to mind. Unaccountably high species numbers of plants occur in southwestern Australia and the Cape region of southern Africa (reviewed in Rosenzweig 1995; Linder et al. 2003), areas that are neither equatorial nor productive nor, it would seem, tectonically active.

As has been noted by many previous authors, some clades are vastly more diverse than others arising at the same time. In general, plant and animal groups that practice internal fertilization (either directly or with the use of animal vectors) are far richer in species than those in which the union between male and female gametes takes place unsupervised away from the parents (see e.g., West-Eberhard 1983). A related pattern is that some geologically younger clades appear to be richer in species, and to be more concentrated in equatorial regions, than older clades (Crame 2000, 2002; Magallón and Sanderson 2001; Davies et al. 2004). Thus, in the sea, veneroidean bivalves are more diverse and more tropical in distribution than are protobranchs (Crame 2002). Host-specialized parasites are vastly more diverse than herbivores and predators with broader diets (Price 1980; Mitter et al. 1988).

Finally, diversity at the regional level seems to have increased over the course of geological time. The best evidence comes from studies of shallow-water communities on the seafloor (Bambach 1977), with large increases occurring during the Cambrian and Ordovician, and during the Cretaceous to Recent interval. Debate rages about whether this local or regional pattern also applies to global diversity. The issue is beset with daunting methodological and statistical problems. Given the difficulty of measuring global diversity in the modern biota, I am skeptical that an empirical pattern in global diversity is meaningful either statistically or in a biological context (Vermeij 1987; Vermeij and Leighton 2003). Nonetheless, there are reasons to expect that diversity in most environments has risen over time. I return to this matter toward the end of this essay.

BUILDING A THEORY OF DIVERSITY

These and many other examples are empirical generalizations of pattern. They are descriptions, phenomenological statements that invite explanation. Variables such as latitude, temperature, productivity, area, and clade membership seem empirically to be related to diversity, but none is perfectly correlated with species number, and the variables are neither independent of each other nor consistently linked. In order to arrive at a more fundamental understanding of diversity, we, therefore, need a theory that accounts for the patterns and that explains exceptions.

The task of creating such a theory requires an understanding of why diversity should arise in the first place, as well as knowledge of the factors that promote and depress it. To gain perspective on this matter, it is important to realize that diversity characterizes all complex systems. Although this essay is devoted mainly to the diversity of species, the notion of diversity can also be applied to human occupations, languages, linguistically distinguishable phonemes, cultures, sources of food, brand names, architectural styles, chemical compounds, cell types, and thousands of other manifestations of variety. Any theory of diversity must therefore not be so specific that it can deal with only one or two of these manifestations. The generality of the phenomenon of diversity suggests that some very fundamental, broadly applicable principles are at work in complex systems that govern not just the diversity of species, but other expressions of variety in the nonliving universe, in the organization of life, and in human affairs.

Elements of such a theory must at minimum include the following: (1) the division of labor, the result of the trade-off principle, which asserts that competition among entities for locally limiting resources promotes specialization because entities cannot perform all functions equally well; (2) the range of possible states, the universe of phenotypes that are potentially available for occupation by some entity in a system; (3) a mechanism for creating change, a necessity if diversity arises from uniformity; (4) opportunity, the set of conditions that enable entities to explore and occupy the universe of possibilities and to create new ones; and (5) constraint, the set of conditions that set limits to, or prevent occupation of, the universe of possibilities.

A prerequisite for diversity is that there exists a universe in which many states are not only possible, but realized. In biology, we might refer to states as phenotypes; in the nonliving world we think of elements, compounds, thermodynamic states, and the like. The universe of possibilities is typically vastly larger than the realized diversity, but at the same time it depends on what already exists. In a world of single-celled prokaryotes, for example, a warm-blooded multicellular mammal would be essentially inconceivable, because there is no mechanism to transform one prokaryote or even a collection of prokaryotes into a mammal in one step or even a few steps. Potential diversity — the range of possibilities — is, thus, dictated in part by the possibilities that have already been realized (Kauffman 2000). The higher the existing diversity, the greater is the universe of possibilities. Key questions are how potential states are generated, how these states come to be

occupied, and which factors limit both the universe of attainable states and the realization of the potential to occupy those states.

In the realm of life, where evolution — descent with modification — prevails as the mechanism of change, diversity arises ultimately as error. Variation arises as an alteration in the genetic code, as an error in replication or as insertion or deletion of code. Genetic error may be phenotypically silent, as it typically is if it involves the substitution of a nucleotide in the third position of the three-nucleotide code for an amino acid; or it may be expressed phenotypically, that is, when the genetic code is translated into physiology or morphology. Meaningful diversity arises only when initial error comes to be associated with a phenotypically meaningful, functional change, that is, with a change that affects the survival or reproduction of the entity bearing it. At the species level, diversity becomes meaningful only when the population in which a change arises becomes genetically isolated from the parent population and from potential sister populations. The creation of diversity is thus all about the emergence of meaning, of phenotypic function that is genetically isolated and distinct from functions in progenitors and contemporaries.

The generation of change and the emergence of meaningful differences depend both on genetic architecture and on the environment in which entities make a living. It is far beyond the scope of this essay to review these matters in detail, but a few points deserve emphasis. First, a genetic and developmental architecture in which several semi-independent modules are loosely linked is critical not just for the origin of mutations or other genetic alterations, but also for shielding such variants from selective removal for a time. Raw variation is, thus, generated and conserved long enough to be available for adaptation (Wagner and Altenberg 1996; Kirschner and Gerhart 1998; Newman and Müller 2001). In a functioning system of parts, most changes are deleterious. If the parts are highly integrated and interdependent, the change would affect the entire system and would therefore jeopardize that system, with the result that the alteration will be lost. If, on the other hand, the parts or modules comprising the system are loosely linked, and thus semiautonomous, a change with short-term, mildly deleterious effects can persist for a longer time, because its damaging effects are spatially limited. The variant may be incorporated in later generations as part of a new beneficial order. Most organisms, ecosystems, and societies at every level from cells to civilizations are organized as semiautonomous, interacting modules, which are variously specialized in function. This style of organization — itself the product of adaptive evolutionary processes — promotes the generation and conservation of variation. With a larger number of types of modules and with greater independence among them, the range of adaptive possibilities — the adaptive versatility of the system — increases (Vermeij 1973; Kirschner and Gerhart 1998; Raff 1996; Newman and Müller 2001; Galis et al. 2001; Galis and Metz 2003).

The environment in which variation arises has three fundamental roles in determining the potential and realized range of phenotypic space. First, it affects the potential range through temperature and the availability of resources. Second, it affects the likelihood of isolation of populations, a necessary condition for the generation of variation at the species level. Third, the realized range of possibilities is affected by competition between entities for locally limited resources. These three fundamental roles are intimately connected through feedbacks between living things and the environments to which life responds and which life creates (Vermeij 2003, 2004).

Almost every physical characteristic and chemical reaction important to living organisms depends on temperature. As temperatures rise from the freezing point of water to values between 30 and 40°C, rates of reaction increase, the activation energy for enzymatically catalyzed reaction decreases, the viscosity of water falls, and the solubility of gases and minerals changes. Accordingly, many functions become less expensive as temperatures rise (e.g., production of a calcareous skeleton, rapid locomotion in water, circulation or conduction of fluids). The range of pos-

sible metabolic rates, growth rates, locomotor speeds, and morphologies related to these rates is much greater when environmental or body temperatures are toward the high end of the thermal range of plant and animal life than when temperatures are 100°C or lower (Vermeij 1978, 2003). As a result, temperature regimes typical of the tropics or of warm-temperate summers are conducive to a much larger universe of phenotypes and lifestyles than are the thermal regimes characteristic of polar regions or the deep ocean.

Similarly, conditions in which material resources are plentiful and predictably available permit a wider range of adaptive possibilities than do conditions of chronic, unpredictable, or periodic scarcity (Clarke 1980, 1983). High metabolic rates and adaptive lifestyles simply cannot be maintained at times of scarcity, and are excluded from the universe of adaptive options for those entities that have no means of overcoming or provisioning against fluctuations in resource supply. Just as low temperatures prevent effective exploitation of abundant resources, so the absence of light for photosynthesizing plants or the unavailability of food for animals will severely constrain life processes even if the thermal environment is highly favorable. Moreover, newly isolated, small populations that would survive under a regime of plentiful resources might perish under conditions of scarcity, and therefore would be prevented from forming the nucleus of new daughter species (Allmon 1992, 2001; Allmon and Ross 2001; Vermeij 1995).

Higher temperatures and a more prolific and predictable resource supply create conditions favorable to the generation and retention of the variants that are essential as raw material for diversity. In human society, this kind of permissiveness is promoted by social tolerance of difference, the acceptance of freedom as a desirable state for individuals and groups, and — in order to realize the potential of individuals' abilities — a high predictability and prosperity of the economy that supports society. Conditions that allow for experimentation, expansion, and freedom without immediate sanction are, thus, essential for generating and nurturing variety (Vermeij 2002a, 2004).

Biologists studying speciation — the evolutionary process that generates diversity at the species level — have emphasized the isolation of populations from parent and contemporary populations as a necessary condition for the creation of new species. Isolation arises either when a previously single, genetically unified population is divided into mutually isolated fragments by some disruptive process, or when individuals from a parent population disperse to an environment not previously occupied by that population. Environmental conditions that increase spatial heterogeneity or promote intermittent dispersal, therefore, favor isolation.

But potential is not enough to explain diversity. There must be factors at work that do not merely permit difference, but that favor divergence. As noted by Ehrlich and Raven (1969), isolation may be a necessary condition for the creation of new, genetically and evolutionarily independent species; but it is not a sufficient one. In addition to isolation, the formation of species entails divergence, which, in turn, implies a regime of selection and adaptation that differs from the regime prevailing in populations with which the isolate could potentially exchange genes. Divergence may require genetic isolation, but it is not an inevitable consequence of isolation.

Competition for locally limiting resources would seem to be a critical agency for selection, and therefore is one factor — perhaps the most important factor — propelling populations to diverge. It provides the key that translates meaningless, often invisible variation into meaningful function. Making a living entails the acquisition and retention of resources. This activity of life takes place in settings where many entities are engaged in the same pursuit. Individuals, or groups of individuals, thus compete. Mechanisms of competition and the resources for which entities compete are themselves highly diverse, and of course are the products of variation and the selective processes acting on that variation. Cooperation, for example, is a highly effective means of competition; so are predation, parasitism, rapid incorporation of nutrients, preemption, aggression, passive defense,

and a hundred other evolved mechanisms. Evolutionarily highly derived plants and animals compete for resources such as mates or dispersal agents that for many other kinds of organisms simply have no meaning.

Because variants tend to differ in how effectively they gather resources or prevent other entities from taking them, a very common evolutionary response to competition is to specialize, either by minimizing competition with other entities or by beating others at their own game. Specialization is enforced by the trade-off principle, which asserts that improvement in one function engenders less effective performance in other functions. As a result, individuals may confine themselves to one or a few resources, or they may specialize to particular occupations, modes of defense, methods of resource acquisition, enemies on which defenses are concentrated, places to live, and so on. The greater the diversity of resources and of enemies, the greater are the scope and pressures of specialization. In short, competition-driven division of labor is the agency that promotes functional diversity; it is the agency that translates potential into realized variety. As Adam Smith (1776) pointed out long ago, greater wealth — that is, greater access to predictable and plentiful energy — makes possible more intense competition and is therefore associated with greater division of labor and with a larger number of occupations. As the thermally- and resource-based potential for the generation of phenotypes increases, so do the advantages of competition-driven division of labor and specialization.

Specialization is not simply an adaptive response to competition; it creates environmental heterogeneity where previously there was a perceived sameness. The specialization of an herbivorous insect species, to one particular host species, for example, means that one plant is not like another. If locally limiting resources provide conditions favorable to host-specific specialization, the environment for the specialist is patchier than that same environment would be for the specialist's more generalized ancestor. There is, in other words, a positive feedback between the generation of variety — through heterogeneity and isolation in this case — and the realization of potential variation, in this example through competition-driven divergence and specialization. In short, environmental heterogeneity and the potential for isolation are not just manifestations of the physical and chemical heterogeneity of the world; to an important degree, they are created by organisms themselves.

Competition creates feedback between realization and potential in still another way. The "exploration" of phenotypic space is not merely a passive process or a passive consequence of randomly generated variation; it reflects successful, adaptive, realized solutions to challenges that are ultimately imposed by competitors. The envelope of possibilities thereby enlarges, and this, in turn, provides the raw phenotypic material for still further charting of new phenotypic territory. For example, higher metabolic rates provide substantial competitive advantages to entities as long as resources are plentiful and predictable enough to sustain them. Rapid metabolism, in turn, permits physiologies and morphologies that are unavailable to organisms with low metabolic rates (Vermeij 2002a). These states would be left unexplored and unrealized in the absence of intense competition and the absence of the resource infrastructure necessarily for the evolution of high metabolic rates.

High diversity in an economic context thus arises when potential differences in performance are large and when the stakes for success — the difference between the benefits of success and the cost of failure — are high. In nature and in human society, competition and diversity appear to be highest when the environment permits the generation and the nurturing of variation (Vermeij 2002b, 2004).

It is important to emphasize that neither competition nor potential is by itself sufficient for diversity. Intense competition will reinforce the status quo and will purge novelty if conditions prevent entities from expanding in size or numbers (Vermeij 1995, 2002b). In order to promote diversity, strong selection exerted by competitors must be accompanied by an ability of entities to

respond to selection. Without that ability — that is, without environmental permissiveness — competition merely stultifies and imposes constraint. Similarly, in the absence of competition, much potential remains unrealized, and the potential universe of phenotypic options will remain largely empty.

Species emerge because members of species can recognize each other. The species is perpetuated through reproduction, which in many forms of life requires mating between two individuals whose genes come together and then recombine to form individuals of the next generation. Correct pairing — that is, pairing of individuals belonging to the same species — requires that individuals distinguish their kind from other kinds.

Species in which mating takes place outside the body of one of the members often have recognition expressed at the level of proteins in the gametes; species with internal fertilization typically have elaborate mechanisms by which adult individuals make the distinctions. With only a few species coexisting, methods of recognition need not be very elaborate; but as the number of co-occurring entities rises, and as population densities for individual species fall, the cost of making the wrong choice increases, and mechanisms ensuring correct pairing can become complex. This is notably the case with internally fertilizing groups. Diversity in these groups — many arthropods, molluscs, vertebrates, and flowering plants — is staggeringly high. As noted by West-Eberhard (1983), even small changes in the reproductive system or the recognition system can lead to genetic isolation of a daughter population from its parent or sister, and so set the stage for speciation if opportunities for the perpetuation of the population exist. The creation of more diversity as recognition systems become more elaborate is one of several mechanisms by which positive feedbacks allow diversity to increase.

All these factors conspire to give diversity a self-propagating quality. Every species is potentially a resource on which some other species can in principle specialize or to which another species must adapt. Moreover, species have the ability to regulate resources, enabling other species to specialize on that resource. Through adaptation, those species that either increase or stabilize the supply of resources create an environment in which the greater commonwealth permits and promotes higher competition-driven diversity (Leigh and Vermeij 2002). The positive feedback that species have on each other therefore amplifies and exaggerates the stimulatory effects that such factors as higher temperatures and greater productivity by themselves have on diversity.

It is the self-propagating property of diversity, together with a general rise in productivity and in competition, that yields the expectation that diversity has increased through time. The argument, as laid out in detail by Leigh and Vermeij (2002), is that species that create conditions favorable to other species as well as to themselves will more often succeed than selfish species. These species will have the effect of increasing the productivity of the ecosystem they inhabit. Increased productivity, in turn, “creates jobs” for other species. Moreover, as species collectively create a more highly regulated physical and chemical environment that is increasingly stable and resilient in the face of external disruptions, rates of extinction of clades tend to decrease through time (for a detailed discussion and documentation of decreasing rates of extinction through time, see MacLeod 2003). Clades with sophisticated recognition systems proliferate relative to clades in which competition for mates is less intense. Environments and regions in which competition and adaptation are least constrained produce the species with the highest competitive, defensive, and reproductive performance. From these centers of innovation and diversification, clades spread out, bringing to more outlying environments and regions increases in productivity and regulation that already existed in the centers. All of these factors conspire to favor increases in productivity and diversity. Occasional reversals at times of major extinction briefly interrupt, but do not fundamentally alter, this expected trend (Vermeij 1999, 2004).

A final factor contributing to the positive feedback between productivity and a rise in diversity through time is mobility, which enables rare species to persist. As Leigh (1999) has emphasized, the great majority of species in highly diverse rain forests are rare, being represented by widely scattered individuals. This is equally true of species on reefs. In Leigh's interpretation, rarity of many rain-forest tree species may be enforced by specialized enemies, whose effectiveness greatly decreases as the distance between nearest neighbors increases (Janzen 1970). In general, small populations of widely scattered individuals are susceptible to extinction because, in sexually reproducing species, individuals cannot easily find mates and so may be unable to reproduce. Rarity is made possible in part by a combination of high mobility and the capacity to identify and locate members of the same species at a distance. For flowering plants, which as adults do not move, mating is often facilitated by highly mobile pollinators. Without these animal helpers, flowering plants could not maintain populations of low density, because mating through wind- or water-pollination becomes highly inefficient as the distance between nearest neighbors increases (Raven 1977; Regal 1977). Animal mobility entails relatively high metabolic rates, which are sustainable only if the availability and reliability of primary production are sufficient to support substantial populations of consumers. As productivity generally rises through geological time thanks to intense competition and collective, ecosystem-level regulation of resources, an increased emphasis on mobility enables more and more species to coexist and to maintain small populations of widely scattered, sexually reproducing individuals. Altogether, then, there exist powerful positive feedbacks among productivity, enemies, mobility, and diversity.

The foregoing thoughts can hardly be considered a full-fledged theory of diversity, but I hope they will pave the way to a more formal proposal. Diversity is a phenomenon rich in patterns and complex in its causes and consequences. What we need now is a fundamental understanding of the phenomenon based on the laws of economics, organization, and evolution.

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Development, Ecology, and Environment in the Cambrian Metazoan Radiation

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The Cambrian radiation of animal life is one of the most profound episodes of evolutionary innovation in the history of life. Understanding the causes of this event requires deciphering the relative contributions of environmental triggers, developmental novelties, and changes in ecosystem structure. At present, ecology appears to have been largely responsible for the breadth and structure of this event, but we lack adequate, process-based models to understand these ecological dynamics.

The rates and causes of many episodes of evolutionary innovation remain poorly understood, in large part because we lack adequate process-based models to understand these events. Developing such models is particularly difficult because several of the most interesting episodes of evolutionary creativity involve changes in the physical environment, the establishment of new ecological dynamics and often changes in genetic and developmental information processing. Integrating the three components of this evolutionary triad is demanding, and developing process-based models to understand the range of potential contributions of each leg of this triad is even more challenging.

In this contribution, I want to explore how we can develop greater understanding of evolutionary innovation, using as my example the Cambrian metazoan radiation, which is the explosion of animal life beginning about 575 million years ago that resulted in the appearance of most of the major groups of metazoans. The question I want to address is the role of environmental, ecological, and developmental forces in producing this incredible increase in biodiversity in a relatively short amount of time, at least by geological standards, if not ecological standards. Although there has been a remarkable increase in our understanding of the conservation of developmental mechanisms across metazoans, it looks like the primary factors driving this diversification are ecological. However, I will argue they are ecological in a way that we do not really understand. We do not yet have models allowing us to appreciate the dynamics of this process. A real understanding of events in the Cambrian radiation will require the generation of such models, testing them against fossil and other data and progressively refining them.

EVENTS OF THE NEOPROTEROZOIC-CAMBRIAN TRANSITION

There is a diverse fossil record that precedes the events of the Cambrian explosion. Prior to about 575 million years ago there was a very diverse fossil record of a variety of microfossils and algal groups (for reviews, see Knoll and Carroll 1999; Valentine et al. 1999; Valentine 2002). These include testate amoebae, red and green algae and a variety of spiny, organic-walled microfossils of

uncertain affinities known as acritarchs (Javaux et al. 2003). The very earliest impressions that have been interpreted as possible animals are the *Twitya* disks from the McKenzie Mountains in northern Canada. These enigmatic discoidal fossils appear somewhere between 610-600 million years ago, during a period of glaciation in the late Neoproterozoic. More convincing animal fossils are found in the Doushantuo Formation of southern China. Dating to 590-570 million years ago these include a suite of demonstrably metazoan early embryos, along with a variety of algae and acritarchs (Fig. 1). The exciting thing about this phosphorite deposit is the exquisite preservation of fine cellular detail (Xiao et al. 1998; Xiao et al. 2000; Chen et al. 2002).

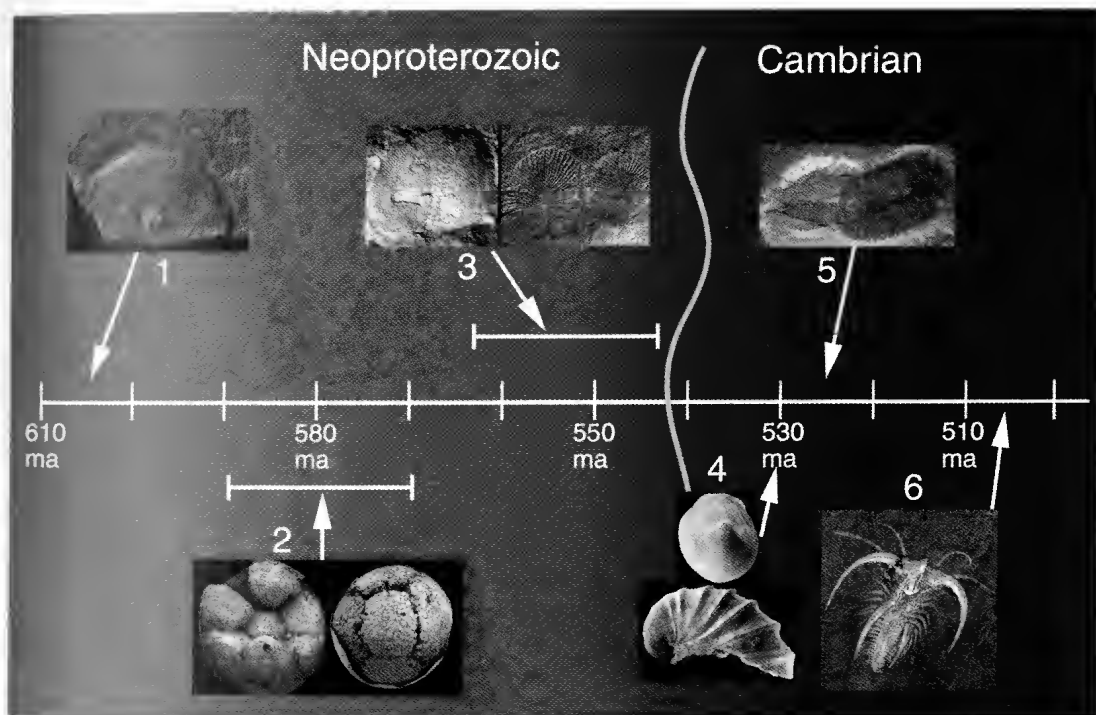


FIGURE 1. The pattern of evolutionary events across the late Neoproterozoic-Cambrian boundary, with some of the distinctive fossils of this interval. (1) Earliest putative metazoans, the *Twitya* discs of the McKenzie Mountains, Canada. (2) Early embryos of the Doushantuo Formation, China. (3) The Ediacaran fossils of the latest Neoproterozoic. (4) Small shelly fossils of the Tommotian Stage of the Early Cambrian. (5) *Fuxianhuia* from the Lower Cambrian Chengjiang Fauna, Yunnan Province, China. (6) The primitive arthropod *Marella* from the Burgess Shale, Canada. Photos of the Doushantuo fossils from Shuhai Xiao, with permission.

Soon after the appearance of the Doushantuo fossils the Ediacaran fauna appears. First discovered in southern Namibia, but most strongly identified with the Ediacaran Hills of South Australia, elements of this assemblage of disks, fronds and other radially and bilaterally symmetrical fossils has since been recovered from many different parts of the world, including the White Sea in Russia, eastern Newfoundland, and the Yangtze Gorge in south China (Gehling 1991; Seilacher 1999). Although the taxonomic diversity of this assemblage is increasingly well understood and the taphonomic conditions under which the fossils are preserved have been exhaustively documented, the evolutionary development and phylogenetic affinities of these taxa remain highly contentious. Some paleontologists have suggested the segmented forms such as *Dickinsonia* may have affinities with annelids, other with arthropods, echinoderms and other groups. Such phylogenetic assignments, if correct, suggest that the origin of the Bilateria lay before the Ediacaran assemblage, and

that each of the major bilaterian clades had already diverged as well. The difficulty with this view is that the similarities between Ediacaran fossils and bilaterian phyla are largely superficial with few diagnostic synapomorphies supporting the assignments. Indeed, most Ediacaran fossils appear to be of cnidarian grade, with no evidence for appendages, mouth, eyes, or other advanced morphological features. That the bilaterian Metazoa predate 555 million years ago is fairly certain, given *Kimberella*, a distinctive bilaterian fossil found in the White Sea (Martin et al. 2000). Although molluscan affinities have been suggested for *Kimberella* (Fedonkin and Waggoner 1997) this remains uncertain. The most one can comfortably claim is that it is bilaterian. The phylogenetic affinities of the remaining Ediacaran fossils are more problematic. Thus, it is entirely possible that, whereas, bilaterian groups had appeared in the late Neoproterozoic, none of them belongs to the extant bilaterian clades. The critical issue, as discussed further below, is the age of the last common ancestor of the two great bilaterian clades, the protostomes and deuterostomes.

Finally, after about 550 million years ago, the earliest skeletonized fossils appear as simple tubes and cones in Namibia and elsewhere. Thus begin the events of the real Cambrian radiation, with an increase in the diversity and complexity of benthic trace fossils at the base of the Cambrian, an increase in acritarch diversity and abundance, then near 530 million years ago a fairly dramatic appearance of small skeletal fossils, molluscs and brachiopods, followed by the first trilobites. Also in the Lower Cambrian are found the wonderful soft-bodied fossils of the Chengjiang fauna in China, then the Middle Cambrian Burgess Shale in British Columbia. By the end of the Lower Cambrian, evidence from the Chengjiang suggests that chordates, and possibly even vertebrates had appeared, along with elements of every durably skeletonized phylum except the bryozoans. These latter two deposits provide a unique window into the soft-bodied fossils of the Cambrian radiation, demonstrating that the diversity of poorly preserved animals was as great as the diversity of those groups with skeletons.

These biological events did not occur in a vacuum, but were intimately connected to a number of changes in the physical environment. A number of distinct glaciation events occurred near 600 million years ago, although the correlations between them remain ambiguous and hence the number of glaciations remains unclear. Glacial diamictites, with large boulders and pebbles encased in very fine-grained sediment, are a very distinctive component of these glacial intervals, but they are often accompanied by the diagnostic cap carbonates. These carbonate deposits, with a clotted texture, radiating aragonitic fans and other unusual features, are found immediately overlying many of the glacial deposits. These and other features have perplexed geologists for several decades. The Snowball Earth hypothesis of Harvard's Paul Hoffman and Dan Schrag is the most challenging explanation (Hoffman et al. 1998, Hoffman and Schrag 2002). They argued that the glacial events of the Late Neoproterozoic involved a complete freezing of the Earth from pole to equator covering the planet in a blanket of ice. The ice persisted until volcanoes released enough carbon dioxide to trigger a rapid greenhouse effect, melting the ice and generating a brief period of acidic oceans.

The diversification of animals happened in the aftermath of the last of these glaciations and Hoffman and Schrag have suggested that the environmental events triggered the Cambrian radiation. Whereas the temporal correlation is correct, whether or not the Snowball Earth hypothesis is likewise correct remains highly contentious among geologists (e.g., Ridgwell et al. 2003; Hyde et al. 2000). It does appear to be the case that many of these glacial diamictites were deposited at low latitudes and it is difficult to see how low latitude glaciers could occur close to sea level without completely freezing the oceans. However, some of the glaciations appear to be very short-lived (Thompson and Bowering, 2000). This poses a problem because the build-up of volcanic carbon dioxide in the atmosphere is believed to end the Snowball Earth events. If the glaciations are too

short, insufficient time will have elapsed for sufficient volcanism, and some other cause is required to end them; or they were not Snowball Earth events.

The critical issue is what the effects these environmental changes had on biodiversity. We do have one way of considering this question, which is to look at recoveries after other major mass extinctions. If you do that, for example, if you look at the Early Triassic after the end-of-Permian mass extinction 251 million years ago, we do not see the extent of morphological innovation that we see in the Cambrian. This and other lines of evidence suggest that although these sorts of environmental factors may be temporally coincident, it is highly questionable that they were both necessary and sufficient for the breadth of the Cambrian radiation.

Glaciations were not the only dramatic events during this interval. Although the only means of documenting changing oxygen levels in the atmosphere are indirect, there is at least suggestive evidence that the amount of oxygen may have risen rapidly in the latest Neoproterozoic (Knoll and Holland 1996; Knoll and Carroll 1999). Collagen is a characteristic protein of animals but synthesizing the protein requires higher levels of oxygen than seemed to have been present for much of the Proterozoic. Other changes in ocean chemistry seem to have occurred as well (e.g., Canfield 1998).

Very sharp negative shifts in the carbon cycle occur throughout the late Neoproterozoic, often associated with the glacial events (Kaufman et al. 1997). Using these isotopic shifts as markers of glaciation is perilous, as many other causes can trigger such isotopic excursions. New evidence from Oman suggests that a very dramatic shift at the base of the Cambrian may reflect a catastrophic mass extinction (Amthor et al. 2003), in turn suggesting that the Cambrian radiation may, at least in part, be coincident with a post-extinction biotic rebound.

One of the challenges of understanding the causes of the Cambrian explosion is sorting out the causal connections, if any, between the environmental changes and the pattern of biological innovation. Many of these environmental events have been implicated, largely by non-paleontologists, as the driving factors behind this increase in diversity. Mere correlation is not enough, however. To understand these events we need to unravel the causal connections, if any, between changes in the physical environment and the evolutionary consequences.

A BIOLOGICAL PERSPECTIVE ON THE METAZOAN RADIATION

Modern animals provide another window into the Cambrian radiation in several ways. First, morphological and molecular data have revolutionized views of metazoan phylogeny over the past decade. A series of studies has confirmed the presence of three great bilaterian clades of metazoans: the deuterostomes, encompassing chordates, echinoderms, and several smaller groups; two protostome sister clades, the arthropods, onychophorans, and other groups which shed an exoskeleton as the ecdysozoa; and the lophotrochozoa including the molluscs, brachiopods, annelids, sipunculids, and other groups (Adoutte et al. 2000; Aguinaldo et al. 1997; Peterson and Eernisse 2001). Significantly, all of the non-coelomate groups previously believed to have evolved before the protostome-deuterostome split appear, with this new evidence, to have affinities within the ecdysozoa or the lophotrochozoa. These reassignments make the nature of the last common protostome-deuterostome ancestor (PDA) even more critical to interpreting the nature of the Cambrian radiation.

The age of the PDA is the second critical area of biological insight. Beginning with the Wray et al. (1996) analysis, a host of new molecular sequences, better techniques, and more rigorous analyses has been applied to molecular clock studies of metazoan origins. Wray et al. suggested the PDA could date to 1.2 billion years ago. If this is correct, it suggests much of the metazoan diver-

gence occurred long before the Cambrian radiation, which then becomes the appearance of these groups in the fossil record rather than their origin. Subsequent studies have reported a wide range of results for the age of the PDA, from 1.5 billion years to as young as 650 million years (Aguinaldo et al. 1997; Aris-Brosou and Yang 2003; Gu 1998; Hedges et al. 2004; Lee 1999; Wang et al. 1999). One obvious conclusion from such a wide scatter of results is that the methods have yet to converge (Smith and Peterson 2002).

Kevin Peterson has addressed one of the potential problems. Most published molecular clock studies rely on vertebrates (basically fish) as the necessary calibration point to the fossil record. Peterson has shown that invertebrates produce very different results (and this would come as no surprise to any paleontologist), evidently because of systematically different substitution rates between vertebrates and protostomes (Peterson et al. 2004). Molecular clock studies do have the greatest promise for establishing divergence points of metazoan groups independent of the fossil record, and, thus, allowing more robust testing of the correlations between these divergences and changes in the physical environment.

The most exciting biological insights into the Cambrian radiation have come from another source, however, the remarkable discovery of highly conserved developmental genes (see reviews in de Robertis and Sasai 1996; Erwin and Davidson 2002; Erwin 1999; Carroll et al. 2001). A decade ago, few developmental biologists would have predicted that flies and mice used the same genes, and often very similar regulatory circuitry for producing eyes, segmentation, appendages, heart formation, and a host of other morphological features. The Hox complex, responsible for anterior to posterior growth (e.g., Balvoine et al. 2002) and Pax-6, responsible for eye formation (e.g., Halder et al. 1995; Gehring 1996), are perhaps the best known of these highly conserved elements. Such ubiquitous conservation has suggested to many observers that the PDA must have been a relatively complex animal, with a heart, eyes, appendages, complex central nervous systems, segmentation, anterior-posterior and dorsal ventral differentiation, and a complex gut. Such an animal would be hard to disguise from the fossil record if it were benthic and more than a few millimeters long. Even if it were not skeletonized, the trails and other evidence of activity would be preserved. This developmental evidence, thus, appears to be in strong conflict with the molecular clock results.

In 2002 Eric Davidson and I suggested the conflict may be more apparent than real (Erwin and Davidson, 2002). We described an alternative interpretation of many of these developmental genes in which the original role of these conserved genes involved much simpler cell-type specification rather than the current role of complex morphogenetic pathways. Thus Pax-6 may have been involved in producing a photoactive pigment rather than an eye. From this perspective the PDA becomes a much simpler animal. Davidson and I suggested that much of the complex patterns of morphogenesis arose after the PDA, and is thus likely to be specific to individual clades.

BUILDING MODELS

Our expanding understanding of the sequence of events in the fossil record and their connection to changes in the physical environment and of the complexity of developmental innovation has not been matched by a similar conceptual change in understanding the ecological dynamics of the Cambrian radiation. Although there have been many new empirical discoveries about ecological relationships, conceptual advances in the ecological dynamics of macroevolutionary innovation have been missing.

The most conceptually important models of the ecological components of the Cambrian radiation have been those of Valentine (1980; Valentine and Walker 1986) in which niches exist inde-

pendent of the populations that fill them. The model dynamics focus on filling the open ecospace, and the transition between a relatively empty ecospace in which long evolutionary jumps between distant ecologies (and presumably with very different morphologies) are possible, to a fuller ecospace in which competitive exclusion causes a change in the evolutionary dynamics. Whereas such a model may provide useful insights into re-occupation of environments following smaller biotic crises, it is far from clear that it is appropriate to events of evolutionary innovation in which the construction of new niches is an integral part of the event. The issue of niche construction has recently become popular (see Odling-Smee et al. 2003), but there have been few attempts to develop ecological models of the process, or to explore them in a macroevolutionary context (although Ricard Sole and I are currently developing such models). Greater understanding of the ecological dimensions of this triad will require development of such models, exploring their implications for the fossil record so that we can test them, and further refining the models in light of empirical studies.

UNDERSTANDING THE CAMBRIAN RADIATION

Unraveling the causes of the Cambrian radiation requires comparing the relative contributions of the various changes in the physical environment, which, in turn, requires accurate determination of the age of various divergences. The complex changes in ocean chemistry seem most likely to have been associated with the Cambrian radiation, although these chemical changes may well reflect the biological event rather than trigger them. The three other events highlighted here (Snowball Earth, changes in atmospheric oxygen levels and the sharp carbon excursion at the base of the Cambrian), may explain the timing of the radiation, but we have no theoretical basis to suggest that any of the three could produce either the rate or the extent of the innovation.

Establishing the significance of the various developmental innovations in early Metazoa requires placing these innovations in an accurate comparative phylogenetic framework through analyses of a wide range of relevant taxa. Even more important, however, will be greater understanding of the significance of highly conserved genes. Does such conservation, and even conservation of entire regulatory networks imply, as many have suggested, conservation of morphological outcomes or might these conserved genes have been playing a simpler role in the protostome-deuterostome ancestor? In either case, the facts that the developmental toolkit was unequivocally established in the PDA and that the PDA probably lived prior to 555 million years ago strongly suggest that developmental innovation may have been necessary but cannot be a sufficient cause of the main Cambrian radiation after 530 million years ago. The developmental innovations were a precondition to the later events and may explain the extraordinary breadth of the radiation, but not the triggering of the event itself. Indeed one of the most surprising implications of recent comparative developmental studies is the discovery that far-reaching developmental repatterning occurs relatively frequently. As with most other forms of mutation, the rate of production is far greater than can generally be accommodated by ecological and evolutionary demand.

It appears increasingly likely that the causes of the Cambrian radiation lie with the ecological dynamics of positive feedback that facilitated the generation of many new niches. Critical to understanding this event must be the realization that this event did not involve the filling of an empty ecospace, a metaphor that implies the prior existence of a range of niches awaiting inhabitants. Resources certainly existed, but the biological dimensions of how the resources would be divided by new species were not. Generating these new niches was likely a highly contingent process. The positive feedback element of this process involved the formation of new resources, and new niches, as the radiation progressed. Many questions about this process remain unresolved and process models seem required to suggest the course for more empirical studies. These questions include:

How are new niches created rather than filled? What drives the positive feedback component of an evolutionary radiation and what factors eventually limit further rapid increases in diversity? If, as suggested above, developmental innovations are common and ecological potential limits their viability, what dynamic drives this interplay between ecological and developmental innovation? Finally, how do the processes involved in these episodes of evolutionary innovation differ from those associated with other periods of evolutionary change? Changes in developmental innovation seem unlikely to be responsible, suggesting a change in ecological dynamics is responsible? If so, does this imply that one distinction between macroevolution and microevolution may lie in the evolutionary context of the event itself?

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Plant Biodiversity Partitioning in the Late Carboniferous and Early Permian and Its Implications for Ecosystem Assembly

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Terrestrial ecosystems of the late Paleozoic form a distinct global hierarchy of organizational levels, paralleling that seen in the modern world. At the highest level are at least three biotic provinces delimited by geographic and very broad scale climatic factors. Within each province are several biomes, reflecting substrate and climatic controls. Biomes are roughly equivalent to plant “species pools,” those plants capable of colonizing available resource spaces within the physical area of the biome, and within which many species are roughly ecologically equivalent. Biome boundaries tend to be rather sharp. Within biomes are recurrent species associations, or communities, among which there is significant overlap in composition but that differ in dominance-diversity patterns. These patterns are examined here primarily in ancient tropical systems. The patterns of spatial partitioning of Permo-Carboniferous landscapes conform broadly to those predicted by the unified neutral theory of Hubbell (2001). However, species ecological equivalence is not “global” but rather appears to be restricted to biomes/species pools. The complexity of this hierarchical organization appears to have increased and deepened from the time vascular plants appeared on the land surface in the Late Silurian through the late Paleozoic and beyond. This may be related, in part, to increased “energy” input into the system, driving spontaneous organization of complexity and progressively restricting the spatial scale of species equivalence.

The Late Carboniferous and Early Permian time interval (~ 325–280 million years ago) was the first cold climate interval (glacial age, *sensu lato*) in Earth history where the continents were covered by vascular plants. A time of low atmospheric carbon dioxide, possibly high oxygen, and continental glaciation paralleling that of our modern Earth (Berner 1994; Gastaldo et al. 1996), the Paleozoic is an excellent analogue to the present. As a consequence, the spatial patterns of vegetation distribution during this period are remarkably similar to those of today (Ziegler 1990).

The objective of this paper is to examine broadly these patterns of plant distribution at several different scales, from global biotic provinces to the nature of plant response to differences in local habitat conditions. Such patterns underlie a core debate in ecology about ecosystem assembly: Are there such things as assembly rules? Are plants distributed in what would be, under ideal conditions, an essentially unbroken landscape gradient, reflective only of the individualistic tolerances of particular species, or are there interaction rules among species that lead to patterns of structure at different scales of resolution? Whereas this is in part a question of dynamics, which might be seen as difficult to derive from the fossil record, even the dynamics of extant ecosystems are largely inferred from the analysis of patterns in very short-term data with high levels of back-

ground “noise” (see any of numerous ecological studies, e.g., Hilborn and Mangel 1997, or Hayek and Buzas 1997 for overviews). Thus, the Carboniferous lends itself to the detection of significant patterns just about as well as modern systems. Plus it permits aspects of these systems to be studied over time as well as space, lending an extra dimension to pattern recognition. Thus, the basis to infer process and to test models is greatly enhanced by fossil data.

What follows is an initial examination of these patterns at multiple *spatial* scales. It is in space that these ecological patterns are expressed. The addition of a time dimension extends the analysis in a way that ecological studies of modern systems cannot approach. Temporal data allow a system resolved at a particular scale to be tracked through an extended period of time, such as repetitive examination of interglacial vegetation from one cycle to the next (e.g., Schoonmaker 1998).

THE LATE CARBONIFEROUS FLORA

Landscapes of the Late Carboniferous were dominated by entirely different plant groups from those that comprise most of the biomass in modern ecosystems. This is important and adds to the significance of the analysis because we can generalize even more strongly if we see patterns that affect taxonomically different but ecologically comparable groups of plants. At the highest taxonomic level, there were four Linnaean

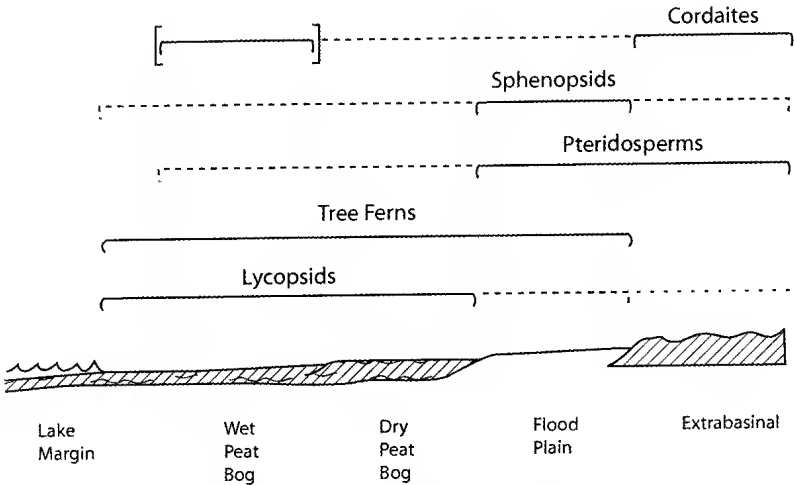


FIGURE 1. Landscape partitioning by major plant groups during the Late Carboniferous. Based on data from the Illinois Basin collected by Pfefferkorn (compression-impression fossils), Phillips and colleagues (coal-balls) and Peppers (palynofloras), from various publications.

classes of vascular plants that were important components of Late Carboniferous ecosystems: lycopids, sphenopsids, ferns, and seed plants. Within these groups were several subgroups, some of which persist to the present. The ecological distributions of these plant groups are summarized in Figure 1.

The lycopids were composed of three orders, all three of which are still extant. The Isoetales, which were represented by the giant lepidodendrid “scale trees,” were dominant biomass producers, particularly in wetland habitats, especially those in which peat accumulated (Phillips and DiMichele 1992). Like extant flowering plants, these ancient lycopids could tolerate both freshwater and brackish water settings, allowing them to colonize all coastal and interior wet areas, forming marshes (DiMichele et al. 1979; Gastaldo et al. 2004a) as well as forested wetlands (Gastaldo 1986). The Lycopodiales and Selaginellales are herbaceous groups today and appear to have had similar roles in the Paleozoic (Thomas 1992). Although accounting for enormous amounts of biomass, the lycopids were not a particularly diverse group, reflecting their growth in a very homogeneous, if extensive, range of habitats — wetlands. Some tree lycopids, however, most notably *Sigillaria*, did grow on drier sandy soils within the broader wetlands, such as those

formed by point bars, that could experience dry intervals. Lycopside were present in each of the major floristic provinces, although different evolutionary lineages are present in each province with little cross occurrence (Meyen 1982; Archangelsky 1984; DiMichele and Phillips 1994).

The seed plants dominated *terra firma* habitats, but were also widespread in wetlands. The most commonly encountered dominant tree groups include the medullosan pteridosperms (seed ferns) in the wet tropics (Phillips 1981; Pfefferkorn and Thomson 1982), and the cordaites (sister group of the conifers) in both the wet and seasonally dry tropics and north temperate zone (Meyen 1982; Raymond 1988; Falcon-Lang and Scott 2000; Falcon-Lang 2003). Less commonly found in basinal lowlands were the conifers (Lyons and Darrah 1989) and the peltasperms (Kerp 1988) in the seasonally dry tropics. In the south temperate zone several distinct groups are found including the pteridosperm *Nothorhacopteris*, ginkgophytes, cordaites, and conifers, though of types distinct from the walchians of the equatorial region (Archangelsky 1984; Archangelsky and Cuneo 1991). The glossopterid floras did not develop in the south temperate regions until the Permian (Cuneo 1996). There are many other groups of seed plants that were not trees but were important ecosystem components, such as the lyginopterids in the wet tropics and a whole array of unique taxa in the seasonally dry tropics.

Important ferns of the Late Carboniferous are divisible into several groups. The most conspicuous of these were the marattialean tree ferns. The Marattiales are still extant, although none of the modern forms are trees. This group dominated tropical wetlands in the latest Carboniferous. These trees were inexpensively constructed in terms of carbon biomass allocation, with stems, leaves, and especially the roots of the trunk-supporting root mantle, rich in airspaces. Inexpensive construction, combined with massive reproduction, permitted the earliest species of this clade to play the ecological role of opportunists though they later rose to ecological prominence to the status of dominant forest trees following extinctions within the Late Carboniferous (Phillips et al. 1974; Pfefferkorn and Thomson 1982; Lesnikowska 1989; DiMichele and Phillips 2002). Marattiales appear in the south temperate regions in the Permian (Cuneo and Archangelsky 1987). Small ferns are assignable to the Filicales (though with organization quite different from extant members of that group, Phillips 1974) and the Zygopteridales, a wholly extinct group (Dennis 1974), in the tropics. The small ferns occupied a wide range of ecological roles, including ground cover and vines, and many were opportunists responding to local disturbance (LePage and Pfefferkorn 2000).

Calamitean sphenopsids of the Carboniferous are very similar in gross structural organization to modern Equisetales, except for the presence of secondary xylem, permitting the Carboniferous forms to grow much larger. This group occupied a very narrow range of habitats, primarily those of aggradational or disturbed settings where their clonal growth habit would permit recovery from burial by sediment accumulation (Gastaldo 1992; Pfefferkorn et al. 2001). Possibly reflective of the narrowness of their habitat, they appear to be depauperate in species diversity throughout their geological history. These plants also were a constituent of the swamps, coexisting in space and time with everything from the "wettest" to the "driest" lycopsids. (Gastaldo et al. 2004b).

Many of these Carboniferous plant groups have relatively closely related modern descendents, although these descendents are very dissimilar architecturally and therefore ecologically (in the sense of Hallé et al. 1978). From reproductive and anatomical points of view, the giant lycopsid trees, in particular have no comparable morphological analogues, and no close phylogenetic relatives still important in modern ecosystems. Modern *Equisetum*, although not woody or arborescent, is very similar to the ancient calamites in basic architecture, including narrow ecological breadth. However, today's floras have architecturally similar plants that use ecospace in a similar manner to the extinct forms (Hallé et al. 1978; Pfefferkorn et al. 2001). This similarity allows us to compare the reaction of flora and vegetation over long time intervals on a "taxon-free," ecomorphic basis.

BIODIVERSITY PARTITIONING

Global Provinces

The largest geographical scale of biological partitioning is the province, which has both spatial and temporal ranges (Wagner 1993). There have long been considered to be three fundamental Carboniferous plant biogeographic provinces (Fig. 2), following the terminology of Raymond et al. (1985; Raymond 1996), with more traditional terms in parentheses (Gothan 1937; Halle 1937; Chaloner and Lacey 1973; Chaloner and Meyen 1973): Equatorial (Euramerican-Cathaysian), Northern High Latitudes (Angaran) and Southern High Latitudes (Gondwanan). In addition, a southern Paratropical floral zone has been recognized recently in the Early Carboniferous (Paracan realm; Iannuzzi and Pfefferkorn 2002). The small number of biogeographic provinces recognized in the Permo-Carboniferous is likely a consequence of the continental configuration of the time. The aggregation of most of the Earth's continental landmasses into a single, nearly continuous region provided opportunities for lateral extensions of plant ranges within, and occasionally between, paleoenvironmentally suitable regions. In the modern world, by contrast, the hyperdispersion of the continents presents many natural barriers to plant dispersal and range extension, isolating climatically similar regions. This leads to the evolutionary independence of such areas and the development of distinct floras.

The Equatorial Province frequently has been subdivided (Fig. 2) to account for persistent differences between eastern areas (Cathaysian), western floras of everwet climates (Euramerican), and western floras of seasonally dry climates (western North American). Clearly, this is a heterogeneous way of dividing up the equatorial region; the two western divisions are cast better as biomic differences within the larger province. In addition, there is clear evidence of spread through time of certain distinctive taxa within the tropics (Fig. 3), indicating that migration routes were

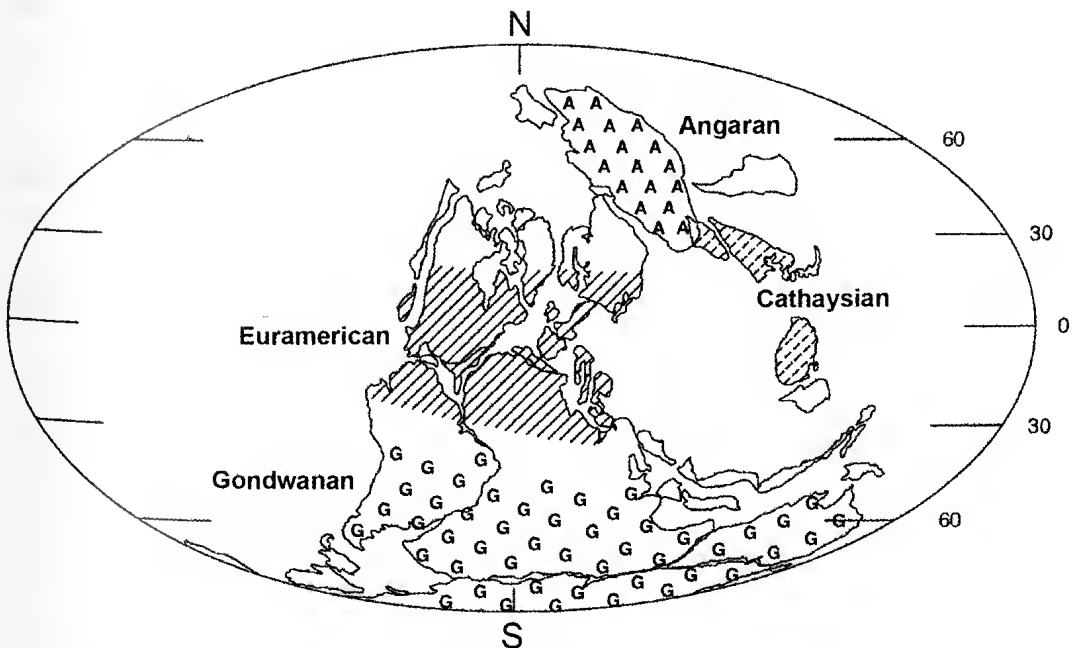


FIGURE 2. The world of the Carboniferous-Permian boundary showing continental positions and distribution of major floristic provinces (base map modified from Eldridge, et al. 2000).

present intermittently, permitting taxa to spread over vast geographic areas within environmental constraints (Laveine et al. 2000). The Cathaysian flora also contains seasonally dry and ever-wet biomes. Both have many generic level similarities to those of Euramerica at the generic level but differ considerably at the level of species. This illustrates the persistent confusion of scale of resolution of these biological patterns. The basic global subdivisions of the Carboniferous persist into the Permian, although more subzonation frequently has been recognized (Chaloner and Meyen 1973; Ziegler et al. 1981; Rees 2002; Rees et al. 2002).

Regions of overlap between these provinces occurred along their contact zones and have been well documented in the Permian. These overlaps occur primarily along the margins of the Tethys Ocean and in other parts of the margin of the Equatorial Province (e.g., Wagner 1959, 1962; Broutin et al. 1995; Broutin et al. 1998). In these areas, mixtures of plants common to seasonally dry areas of the different provinces appear to be the most commonly intermixed taxa and to penetrate most deeply into adjacent provinces. One of the most significant interprovincial migrations (Fig. 4) may be the movement of the ancestors of *Glossopteris*, a dominant in Early Permian age temperate floras of the Southern Hemisphere, from their sites of tropical origin in better drained, extrabasinal floras (Leary 1998).

Provincial regions differed in botanical composition at the level of orders and families, with class-level evolutionary lineages having similar ecological patterns of distribution in each area. The Equatorial Province is by far the best studied, a consequence of the concentration of workers and the accessibility of plant fossils exposed in the course of mining Carboniferous coals. Although the dominate ecosystems are considerably different. Members of the class Lycopsidea are most abundant in wet habitats in all three regions, with seed plants of the Spermatopsida dominating in *terra firma* environments. Small ferns, mostly Filicales, can be found as opportunists, particularly in *terra firma* settings. The Marratiales begin as small, probably opportunistic forms, later becoming

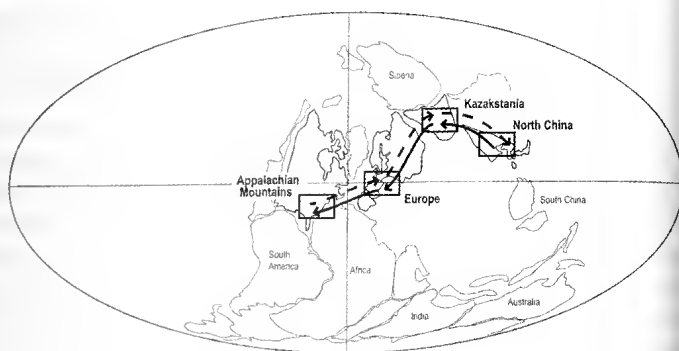


FIGURE 3. Sweepstakes migration route within the Late Carboniferous tropical wetlands. Migration occurred in both directions and included several taxa. Geographic barriers on the route often delayed migration of specific taxa for millions of years whereas others passed through "instantaneously" in geological terms. The four boxes show the areas from which extensive data sets have been published (modified after Laveine, et al. 2000).

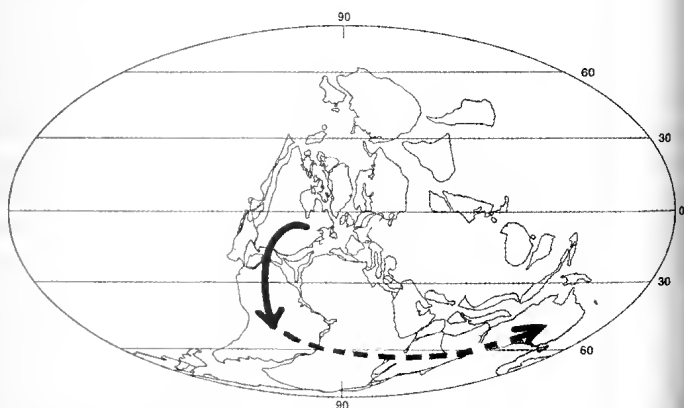


FIGURE 4. Migration route of Late Carboniferous tropical Euramerican plants into the southern temperate Gondwanan realm, suggested for the *Lesleya-Megalopteris-Glossopteris* complex, near the Carboniferous-Permian boundary (reconstructed from interpretations of Leary 1998).

dominants in wetlands. The calamitean Sphenopsida are of low diversity and most common in stream-and-lake margin deposits.

The specific lineages of these plants are generally quite different in each province. For example, the stigmarian (rhizomorphic) lycopsids, *sensu* DiMichele and Bateman (1996), are the dominant elements in most Equatorial Carboniferous wetlands, especially those that accumulated peat, up to the end of the Westphalian. Dominant lycopsids in the higher latitude provinces (including the Paracan realm) were primarily cormose isoetaleans, even if of tree stature. Equatorial seed plant lineages of the Carboniferous include the medullosan pteridosperms, the lyginopterids, the callistophytales, the Euramerican cordaites and their sister group, the walchian conifers, the latter groups demonstrating abundance in seasonally dry habitats (Cunningham et al. 1993). In contrast, ruforian cordaites rose to dominance in the Northern High Latitudes beginning in the mid-Carboniferous (Meyen 1982). In the Southern High Latitudes the appearance of glossopterid seed plants did not occur until the Permian (Cuneo 1996). Among the sphenopsids, the sphenophylls were most common and diverse in the Equatorial Province. Ferns were opportunists in all three provinces, and the marattialean tree ferns (*Psaronius*) are known from the Equatorial Province in the Carboniferous and Permian but also appear in the Southern High Latitude Province in the Permian.

Thus, at the highest levels, the floras of these Late Paleozoic provinces appear to be distinct at a deep evolutionary level with rare crossover taxa, such as the proposed *Lesleya-Megalopteris-Glossopteris* complex. Perhaps this represents different radiations from common Late Devonian or earliest Carboniferous ancestral species lineages.

Biomes within Provinces

The floras that characterize different floral provinces (different physical parts of the globe) can be broken down into sub-floras, or biomes, that characterize different climatic regimes and, possibly, different substrate conditions (Ziegler 1990; Rees 2002). The best example of this is found in the western part of the Equatorial Province (i.e., present day western North America). In this area, three distinct vegetation types have been identified that have few species in common. Two of these, in particular, are well known and characterized. We will refer to these as the wetland biome and the seasonally dry biome (DiMichele and Aronson 1992). The third biome, one of xeric areas with limited soil moisture, is known from a few Permian deposits formed during times of extreme drying in basinal lowlands (DiMichele et al. 2000). This flora probably was present in the equatorial regions during the Carboniferous but in areas remote from basinal lowlands, where preservation was not likely (Lyons and Darrah 1989).

Ziegler (1990), following Walter's (1985) concept of modern biomes, hypothesized that the Permian world was divided in much the same way as today. Using climatically sensitive sediments, Ziegler (1990) identified climate zones and mapped floras onto these. Although his analysis is focused on the Early Permian, the basic patterns described probably would apply equally well throughout much of the Carboniferous. Ziegler et al. (2003) argued that patterns of atmospheric and oceanic circulation created global climatic patterns much like those seen today, and, most importantly, that the boundaries between these climatic zones were relatively sharp. As a consequence of the abrupt climatic discontinuities, there are relatively sharp biomic boundaries.

Continued studies demonstrate that floristic zonation was geographically complex, especially during the Permian (Rees 2002; Rees et al. 2002). Such zonal complexities may reflect the geographical evolutionary roots of floras at the provincial scale (Broutin et al. 1990; DiMichele and Aronson 1992), thus, constraining biomes within specific floristic provinces. The concept of a flo-

ral province is primarily biogeographic. Biomes, on the other hand reflect the climatic-edaphic restrictions on species distributions within provinces, a consequence of both evolutionary and ecological processes.

The plants of the Wetland Biome (everwet biome of Ziegler 1990) comprise the best known Carboniferous flora, and may be one of the best known fossil floras from any time interval in Earth history. Knowledge of this flora derives from its close association with coal beds and, therefore, its exposure in the course of coal mining throughout Europe, North America, and China. The wetland biome includes locally dominant tree forms from five plant lineages in four classes: (1) the lepidodendrid lycopsids of the class Lycopsidea; (2) the calamitean sphenopsids of the class Sphenopsida; (3) the marattialean tree ferns of the class Pteropsida; and (4) the cordaitan seed plants and medullosan seed plants of the class Spermatopsida. In addition, there are many species of ground cover and vines drawn from these same classes. These are the plants so often pictured in classic dioramas of Late Carboniferous lowland, tropical forests.

The Seasonally Dry Biome (summer wet biome of Ziegler 1990) was first described in detail by Cridland and Morris (1963) during a study of plants of the Kansas Pennsylvanian-age coal measures. From the Late Pennsylvanian (Stephanian) Garnett locality, they described a flora dominated by seed plants, most notably conifers, with an admixture of other seed plants. Since that time, there have been reports of a number of other such floras, generally enriched in and dominated by seed plants, including conifers and other genera not found in the wetland biome. The best described of these include the Late Pennsylvanian floras of the Hamilton Quarry of Kansas (Rothwell and Mapes 1988; Cunningham et al. 1993) and the Kinney Quarry of New Mexico (Mamay and Mapes 1992); there are numerous sites that have been collected less intensively but that preserve similar floras in both Europe and North America (Broutin et al. 1990; DiMichele and Aronson 1992). Evidence of the Seasonally Dry Biome is found in Middle Pennsylvanian (Westphalian) coastal wetland deposits well before its more fully developed appearance in the Late Pennsylvanian. The early appearances are diverse in composition. For example, Early Westphalian-age conifer occurrences all occur as rare fragmentary remains apparently transported from better-drained uplands into adjacent basins (Lyons and Darrah 1989). These occurrences indicate, however, that this vegetation existed outside of the window of preservation for perhaps as much as 6 million years before the discovery of extensive conifer-dominated macrofossil deposits. On the other hand, there are fossil assemblages from the Early Westphalian dominated by groups that do not appear to be part of the Seasonally Dry biome, which appears in the later Pennsylvanian. These include floras that have clear substrate/edaphic differences, such as the limestone soil floras described from the Spencer Farm site in Illinois (Leary, 1973, 1974, 1980; Leary and Pfefferkorn 1977), which are dominated by the broad-leaved seed plants of uncertain affinity, *Lesleya* and *Megalopteris* (Fig. 5). Other floras are dominated by cordaites (Falcon-Lang 2003), which were a group that had both lowland, wetland

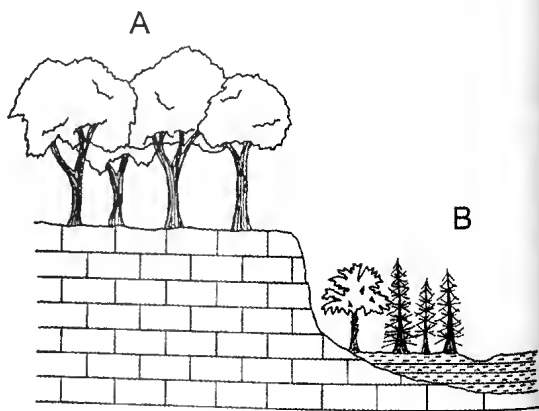


FIGURE 5. Cross section through a reconstructed landscape in western Illinois during the Early Pennsylvanian. A: Extrabasinal, rarely preserved flora growing on limestone soil and experiencing water stress. The trees shown represent *Lesleya* and *Megalopteris*, the presumed tropical ancestors of the south temperate *Glossopteris*. B: Wetland flora here represented by medullosan pteridosperms and *Calamites* (reconstructed after Leary and Pfefferkorn 1977).

species and extrabasinal species (Fig. 6). None of these floras include a conifer component. This indicates that extrabasinal floras (*sensu* Pfefferkorn 1980) were compositionally diverse, indicative of distinct microhabitat differences, possibly reflective of very subtle differences in substrate moisture or even temperature regimes.

The xeric biome was characterized by long periods of dryness and short periods of moisture, based on paleosols and general sedimentary environments (DiMichele et al., in press). Thus, we refer to it as the Seasonally Wet biome. These floras occur in association with bedded gypsums, oolitic limestones, and weakly developed paleosols. It is probable that plants grew along streamsides and significant portions of interfluvies were weakly vegetated or, at times, even un-vegetated. The flora was composed entirely of seed plants, including conifers, cycads, and putative ginkgophytes (DiMichele et al. 2000, 2004). DiMichele et al. (2000) found this flora in rocks of late Early to earliest Middle Permian age in small channel-form deposits of North Central Texas. In taxonomic composition it compares most closely to floras of the Late Permian "Zechstein" flora of Germany and England (Schweitzer 1986) and paleotropical Mesozoic floras of Late Triassic and Early Jurassic age. Consequently, its appearance is precocious and unexpected in rocks as old as Early Permian. A similar Early Permian "precocious" flora has been reported by LePage et al. (2003) that includes elements from both the Angaran and Euramerican floral provinces, which indicates that this kind of biomic partitioning occurred independently in different provinces.

The three tropical biomes share few species in common (Broutin et al. 1990; DiMichele and Aronson 1992). The most prominent crossover species between the Wetland and Seasonally Dry biomes are primarily opportunistic weedy forms of wet soils, such as marattialean tree ferns (Lesnikowska 1989), or streamside specialists adapted to the rigors of periodic catastrophic disturbance, such as calamites (Barthel and Rössler 1996; Gastaldo 1992). The environments these kinds of plants inhabited occurred in nearly all landscapes, but changing climatic conditions reduced the areal extent considerably, from "wetlands" to "wet spots" (DiMichele et al. in press). Between the Seasonally Dry and xeric Seasonally Wet biomes, the common species are primitive groups of conifers. By the time the Seasonally Dry biome appears in the rock record, the western tropical region appears to have been sufficiently dry to exclude virtually all elements from the former Wetland Biome.

Recurrent Assemblages/Communities within Biomes

Within any given biome there are recurrent habitat-specific assemblages that share to a vary-



Figure 6. Reconstructions of the three life forms of cordaitalean gymnosperms from the Late Carboniferous. A: Species from extrabasinal settings on seasonally dry soils (after Grand 'Eury 1877). B: Middle Pennsylvanian species in coastal mangrove environments, often associated with peat formation (after Cridland 1964). C: Late Pennsylvanian species living in peat-forming, nutrient poor wetlands (after Rothwell and Warner 1984).

ing extent species from the larger biome-level species pool. It is at this level that questions of body size also become prominent influences on how community-level dynamics are understood. For example, very small organisms, such as bryophytes and small ferns, may perceive the resource space as more heterogeneous than larger organisms such as trees, shrubs and vines. Here we will concentrate on the larger organisms, those more likely to be preserved in the fossil record in sufficient numbers to be understood in a quantitative sense (Scheihing 1980). In order to elucidate these kinds of distributional patterns, a great deal of collecting and quantitative study is necessary. Consequently, the Wetland Biome of the tropics is best suited to serve as an example.

At the broadest spatial scale, tropical wetlands can be divided into two major landscape types (see Allen 1998, for a discussion of the concept of "landscape"): mostly flooded, swamp environments, and *terra firma* habitats with wet substrates but short or no periods of standing water (Gastaldo 1987). The dominant elements in these two landscape types are very different. During the Early and Middle Pennsylvanian (Westphalian), swamp habitats, often autochthonous or parautochthonous in preservation, were dominated on average by lycopsid trees, with subdominant pteridosperms (Pfefferkorn and Thomson 1982; Phillips et al. 1985; Wnuk and Pfefferkorn 1987; Gastaldo et al., in press). In contrast, *terra firma* assemblages, preserved largely as allochthonous accumulations, were dominated by pteridosperms with subdominant sphenopsids and, late in the Westphalian, tree ferns (Pfefferkorn and Thomson 1982; Scott 1979). During the Late Pennsylvanian (Stephanian), following major extinctions at the Westphalian-Stephanian boundary (Phillips et al. 1974), tree ferns dominated various habitats in both the swampy and *terra firma* parts of the Wetland Biome, with pteridosperms in a subdominant role (Willard and Phillips 1993).

Within each of these broad landscape types a number of species assemblages can be recognized by broad recurrence of dominance-diversity patterns. In the swampy parts of the landscape, peat substrates and clastic substrates, had different suites of dominant lycopsid trees (Willard 1989a, 1989b). In peat substrates themselves, both within and between coals, distinctive recurrent assemblages have been recognized statistically (Phillips and DiMichele 1981; DiMichele and Phillips 1988; Raymond 1988; Willard and Phillips 1993; Pryor 1993). Depending where in time, such communities may be characterized by low diversity and high dominance of specific lycopsids, such as *Lepidophloios*, presumably on flooded sites. In contrast, other communities are rich in ground cover and vines, dominated by a mixture of lycopsids, such as *Diaphorodendron* and *Synchysidendron*, pteridosperms and tree ferns. These plants apparently grew in areas with periodic substrate exposure and associated with elevated levels of charcoal and clastic matter in the coal.

Similar broad plant-by-environment patterns ("biofacies") have been recognized in flood-basin settings (Scott 1978, 1979; Gastaldo 1986). In clastic swamps, dominance by *Lepidodendron*, pteridosperms, and calamites was most common (Pfefferkorn and Thomson 1982; Gastaldo 1987, 1992). Lycopsids were much less abundant in less swampy areas. In nearly all instances, however, there is a great deal of overlap in specific taxonomic composition among wetland habitat clastic deposits. The amount of overlap is variable. Undersampling spatially will make assemblages appear more distinctive whereas, in other instances, local transport of plant parts within flooded wetlands will tend to homogenize assemblages. For example, DiMichele and Nelson (1989) found a sharp contact zone between plant assemblages in the roof shale of the Springfield coal of Indiana, one dominated by pteridosperms, the other by sigillarian lycopsids. On the other hand, Gastaldo et al. (2004b) identified spatial co-occurrence of most of the major plant groups, including different kinds of lycopsids and pteridosperms, in an *in situ* forest in the underclay of the Blue Creek coal of Alabama.

If this discussion appears undefined and lacking in clear structure it is because the degree of species overlap in physical distribution is much greater within biomes, at the scale of communities,

than between biomes. Although there are general patterns of recurrence, there also are degrees of overlap in species distribution patterns that put most in combination at some time and place. The publications cited above document both the local and landscape patterns of differentiation.

DISCUSSION

Where the Action Is

When examined in space, and over a limited interval of geological time, it is apparent that species distributions can be recognized at several hierarchical levels. Our ability to create such organizational spheres, however, begs an important question. Are there processes that operate only at one level or another of the hierarchy? In other words, does the existence of several global species provinces, or of several different biome-level species pools within each province, imply the existence of causation at that same hierarchical level? Are there emergent processes with limited spheres of operation or are there processes that operate at different rates at different spatial scales? The correct answer to these questions might be "perhaps, but not likely."

The alternative is to suggest that processes operating at the level of individual-plant interactions dictate the entire structural hierarchy (Hubbell 2001). In this case, the dominant processes would be inter-individual competition (as opposed to interspecific competition), colonization of temporarily available resource space (following disturbance), and changes in the biogeographic range of populations in response to changes in ambient climatic factors such as rainfall and temperature. In the end, this comes back to the inter-individual factors of differential and directional spatial establishment mediated by competition and opportunity.

It is difficult to demonstrate a need for higher-level processes to create the higher-level spatial patterns. Examine the instance of biomes within provinces, for example. A biome is a collection of organisms with similar climatic and substrate requirements. The limits of those conditions in space will mark the boundaries of the ranges of those species broadly "adapted" to such conditions. And studies of plant geography indicate that climate zones change relatively abruptly in space, not over long gradients (Walter 1985), dictating reasonably sharp boundaries between biomes.

Superimpose on biomes the combined constraints imposed by natural barriers, such as oceans, and major climatic zones, both latitudinal/longitudinal and those created by mountain ranges, and the result is provincialization. Regions with Mediterranean climate, such as southern Europe and coastal California, have been isolated for so long that completely separate species pools developed in each, despite similar physical conditions. This is the interaction of evolution with resource opportunity writ over millions of years. Provincialization may appear spontaneously as the global flora becomes more complex and as natural barriers change over time.

To the extent that there are "emergent properties" of species or individual interactions, these may be found in the controls on community assembly at any given point in space. As Weiher and Keddy (1999) or Belyea and Lancaster (1999) have pointed out in developing models of ecosystem assembly, there are three major components controlling a local flora or fauna. (1) Can individuals of a species get to a site of available resources? Thus, is that species a member of the regional species pool, which is approximately the same as biome? (2) Once dispersed to the site, can those individuals germinate and then utilize the resources effectively, and can they withstand the physical rigors of the particular site? (3) If (1) and (2) are affirmative, can the individuals colonize the site in the face of competition for resources with other individuals, either those that might be there already or others that might enter the site later? This latter point is probably one of population dynamics related both to the efficiency of resource exploitation (e.g., Tilman 1988), and simple likelihood related to numbers of individuals able to find available resources (e.g., Hubbell 2001).

Once established, a species mixture may persist locally simply due to relative proportions of reproductive output by the individuals within a given area. The dominance-diversity hierarchy may be difficult to change without a catastrophic local or regional disturbance because the more abundant species will be the most likely to capture/colonize available space, assuming a general stochastic equivalence among competitors in the face of minor changes in climate and disturbance regime.

As Ulanowicz (1997) has argued, however, once higher levels of system organization appear, these may exert constraints on the dynamics at lower levels. Perturbations, for example, may occur at spatio-temporal scales that are invisible when examined at certain levels of the spatial hierarchy but that, nonetheless, constrain what may or will happen particularly at levels below those where their impact is seen. For example, a climate change may affect the physical distribution of conditions that set the boundaries of a species pool (biome) but may not affect the dynamics of recovery from a local disturbance within that biome. At the same time, changed climatic conditions may greatly change the frequency or magnitude of disturbances at lower ecological organizational levels in the spatial hierarchy.

Self-regulating Properties of Late Paleozoic Ecosystems

It is possible that Late Carboniferous ecosystems had a peculiar form of cybernetic (self) regulation, or one that was more visible in these systems than in those from later periods of geological time (should it prove to be a general ecosystem property, see Drake et al. 1999). This property has been recognized only in the tropical wetland biome where most late Paleozoic paleoecological investigations have focused. In brief, it has been asserted (DiMichele and Phillips 1996; DiMichele et al. 1996; Pfefferkorn et al. 2000; DiMichele et al. 2000) that Late Carboniferous coal-swamp ecosystems retained certain clade-by-environment patterns of dominance, despite a constant background of species turnover of a few percent per 100,000 years, between successive peat-forming wetland ecosystems in geological time (successive glacial-interglacial events). The pattern was first recognized by classifying species according to their ecomorphic characteristics rather than by taxonomically specific characteristics (DiMichele and Phillips 1996), e.g., relative reproductive output, propagule dispersal potential, resource allocation patterns, tree versus shrub versus vine versus ground cover growth habit, and so forth.

There is a clear pattern of ecomorphic replacement within a biome following low level background extinction during the Carboniferous-Permian. This appears to result from ecological limitations imposed by a much older Devonian phylogenetic radiation in which the major plant clades (taxonomic class-level groups) first evolved and developed distinctive ecological centroids (broad environmental tolerances, e.g., wetlands vs. seasonally dry *terra firma* settings) as the evolutionary radiation proceeded (Peppers and Pfefferkorn 1970; DiMichele and Bateman 1996; DiMichele et al. 2000). In this early radiation, all the major body plans of vascular plants appeared — Lycopsidea (in wetlands), Pteropsida (as opportunists in *terra firma* environments), Sphenopsida (in aggradational environments), and Spermatopsida (in *terra firma* environments) — each body plan the equivalent of a traditional Linnaean class. Every group was represented to greater or lesser degrees within each of these broad physical settings, but the dominant clade further subdivided the resource space in a similar manner among lower taxonomic groups, resulting in a kind of fractal pattern. The result was that dominant lineages tended to continue in their particular ecological roles. Extinct ancestors were replaced by structurally and ecologically similar descendant forms within the environments in which they were dominant — such species replacement by close relatives, in response to background extinction, led to conservatism in ecosystem architecture.

The Spatial Limits of Species Substitutability

In a recent book, Stephen Hubbell (2001) developed a new null model for the controls on species assemblage composition. In his model, all species are ecologically substitutable at a global level, interactions are modeled among individual plants rather than among species, and the proportional abundances of species dictate the likelihood of resource capture in response to the disturbances that create opportunities for colonization. The model considers dynamics at the level of both local and regional species pools. The assumption of species substitutability has come under criticism (e.g., Terborgh et al. 1996) because it is clearly incorrect, especially when viewed at a global level. However, Hubbell's thinking developed from years of observing the tree-species composition of tropical forests in which species turnover appeared to be slow and generally non-directional, a pattern he and Robin Foster described as "community drift" (Hubbell and Foster 1986). And when one walks through a forest, even in the temperate zone, it is not clear that a tree on any one spot is competitively favored by the conditions at that point in space. It might be asked if indeed species are not substitutable — but at what spatial scale?

Applicable to this problem is the yet older question of how local species assemblages are structured. Is a local assemblage a happenstance association of species with similar resource requirements under the prevailing climatic conditions, what has been labeled the "individualistic" model? Or are there predictable interactions among species that control the structure of a local assemblage, such that there are distinct emergent properties of the group not present in any of the individual species? The touchstones of this debate are Henry Alan Gleason (1926) and Frederick E. Clements (1916), although the debate has been recast in a variety of terms since, including and extensive debate during the 1970s and 1980s, largely among animal ecologists, about ecosystem assembly (see Diamond 1975). Students of North-temperate Quaternary palynology have strongly reaffirmed the individualistic model by noting that tree species recover from deglaciation at independent rates, resulting in "non-analogue" communities (e.g., Overpeck et al. 1996).

The question becomes, then, is there a scale at which Hubbell's assumption of species substitutability, basic species individuality, applies (given that it cannot apply globally — what are the spatial limits)? The deep fossil record may provide an answer to this question. From our analysis, it appears that the biome is the best approximation of a regional species pool. The regional species pool will contain those species that will be stochastically capable of colonizing a given patch in a local area, allowing for fluctuations in temperature and rainfall and associated disturbance frequency, on a time-averaged basis. We suggest that such species pools might be called "Hubbell cells" in analogy with the Bénard convection cells that develop spontaneously in an open pot of water when heated at the bottom. Species pools may have develop more or less spontaneously across an ecological landscape. This may reflect increased "energy" input to systems over time, created by evolutionary advances in photosynthetic biochemistry, the evolution of complex root systems, and the elaboration of leaves and tree stature.

Such organization of ecological systems in the modern time plane was suggested by Weiher and Keddy (2001), in which they developed a verbal model of ecosystems as thermodynamically dissipative systems, extending to communities concepts previously applied at higher levels of ecological organization (e.g., Ulanowicz 1997). In such systems, levels of hierarchical organization form spontaneously as energy input to the system is increased.

"Hubbell cells" may indeed represent some form of spontaneous ecological organization formed by the interaction of higher-level geographic barriers and lower level, individual processes of competition and dispersal in response to disturbance. "Energy" input to the Earth's global ecological system through time might be conceived as increased efficiency of such things as photo-

synthesis, nutrient cycling, and organismal-Earth system buffering, all of which have changed directionally over geological time. All would increase both the organic and inorganic nutrient pools available to plants. The result has been increasing provincialization through time, there initially being very few global provinces with few and very widespread taxa. This provincialization at the highest level was accompanied by increasing complexity within provinces (biomes) and increasing complexity of plant distribution within biomes. It is at the biome boundaries that most plant ranges appear to truncate and it is within biomes that "individualism" seems to operate to some spatio-temporally variable degree.

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Comparison of Mammalian Species Richness and Community Structure in Historic and Mid-Pleistocene Times in the Colorado Rocky Mountains

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We used an exceptionally rich mid-Pleistocene paleontological sample from Porcupine Cave, South Park, Colorado, to study long-term patterns of species richness and ecological structure in local mammal communities. The fossil data were compared with historic species richness patterns (prior to impacts by humans in the last two centuries) in order to assess whether the many climatic and other environmental changes that have occurred since the mid-Pleistocene significantly affected the numbers of species in various size and trophic categories. After accounting for potential sampling biases, we found remarkable similarity in species richness and community structure between a ca. 850,000-year-old mammal community and the historic one, which suggests that this high elevation Rocky Mountain community exhibited long-term cohesiveness — on the scale of hundreds of thousands of years — in overall species richness as well as in the number of species within various size and trophic categories. Superimposed on this long-term similarity were minor fluctuations in species richness on shorter time scales and changes in species identities through time; some of these shorter-term fluctuations may have been in response to environmental fluctuations. We suggest that species richness and its distribution across size and trophic categories may be a useful metric in assessing the degree to which communities are perturbed from a long-term baseline.

The past few decades have seen significant advances in studies of Earth's biodiversity at scales ranging from genes to whole ecosystems. In part, the explosion of information has arisen from efforts to document existing diversity and to recognize or predict how humans affect ecosystems. Prediction of ecosystem response has been complicated by a lack of knowledge of how biodiversity changes in systems that are not dominated by humans. In other words, what are the normal fluctuations that non-human dominated ecosystems experience in biodiversity metrics? And is any given ecosystem now within or outside those normal fluctuations?

Here we compare paleontological and historic data to explore whether biodiversity changes or remains stable in Rocky Mountain ecosystems over ~850,000 years. We focus on mammals as our indicator of ecosystem change, regarding them as an important component of the communities of which Rocky Mountain ecosystems are composed. Hereafter, we refer to this component of the ecosystem as 'mammal communities', following Brown and Lomolino (1998:627–628) in the definition of a community as "an assemblage of organisms that live in a particular habitat and interact

with one another", and an ecosystem as "the set of biotic and abiotic components in a given environment". Other definitions of these terms differ in details, but agree in principle with the definitions we use (for example, Whittaker 1975). Our metrics for assessing biodiversity are overall species richness of mammals and species richness in various trophic and size categories within the mammal community. Results from our study area suggest that in the absence of significant human impacts, such metrics varied within a relatively small range. We discuss the implications of this finding for ecological theory and for conservation issues.

MATERIALS AND METHODS

We compared species richness, size structure, and trophic structure of two communities separated by ~850,000 years, but from the same place: South Park, Park County, Colorado, at an elevation of ~2900 m (latitude 38°43'45"N., longitude 105°51'41"W, Gribbles Park 7.5' Quad) (Fig. 1). The ~850,000-year-old sample was derived from the mid-Pleistocene fossiliferous deposits of Porcupine Cave, a complex system of well-known localities that has been comprehensively reported elsewhere (Bell and Barnosky 2000; Barnosky 2004a; Barnosky et al. 2004a). 'Mid-Pleistocene' in this paper refers to the medial part of the Pleistocene, not to placement within formal chronostratigraphic nomenclature.

For the fossil sample, following the logic detailed in a previous publication (Barnosky et al. 2004a), we combined specimens from two of the 26 Porcupine Cave localities to generate a robust sample of mammals that lived within an 8–18 km radius of the fossil deposit. The two localities were the Badger Room and stratigraphic level 4 of the Pit Sequence. Fossils in the Pit Sequence include >7000 identifiable specimens (1154 from level 4) that are interpreted as having been accumulated primarily by wood rats (*Neotoma*) dragging in bone-laden carnivore scat and raptor pellets (Barnosky 2004b). Bones in the Badger Room (>13,000 identified specimens) accumulated in part due to the activity of wood rats, but also from the collecting activity of medium-sized carnivores such as canids and mustelids (Shabel et al. 2004), which increased the sample of larger mammals.

Biostratigraphy, sedimentology, amino acid racemization, and paleomagnetic evidence indicate that the two localities are about the same age, between ~800,000 and 900,000 years old (Bell and Barnosky 2000; Barnosky and Bell 2004; Barnosky 2004a, Shabel et al. 2004). Sedimentologic and biotic evidence suggests that the fossil communities existed during a glacial episode, most likely oxygen-isotope stage 22, but possibly oxygen-isotope stage 20 (Barnosky et al. 2004a). The biostratigraphic and paleomagnetic data make it extremely unlikely that a substantially younger or older glacial stage is represented. By comparing a fossil community from a glacial time to a historic community of the present interglacial, we maximized the chances of finding differences between the communities of the two time slices. Therefore, any indications of similarity should be robust.

Detailed radiocarbon dating of fossil deposits that are younger than those of Porcupine Cave, but that are taphonomically analogous (Hadly 1999; Hadly and Maurer 2001), suggests that time-

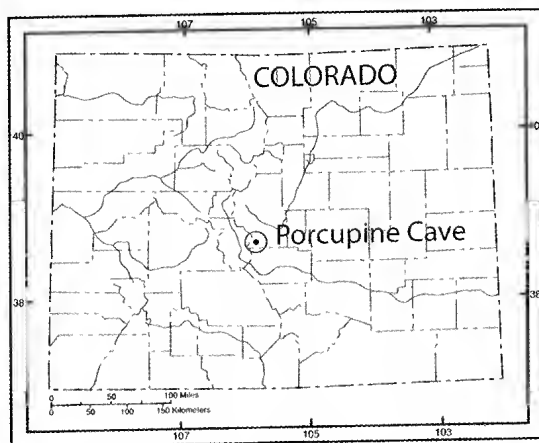


FIGURE 1. Site of Porcupine Cave, South Park, Park Co., Colorado.

averaging in the Badger Room and Pit level 4 is less than 5000 years and potentially as little as a few hundred years. By combining the Badger Room and Pit level 4 deposits, we may increase the amount of time-averaging. However, the assemblage of mammals in the Pit is similar from level 4 through level 8, suggesting that counts of species would not be affected much even with increasing the time-averaging substantially above what we have assumed. For our purposes time-averaging is, in fact, a sampling advantage, because previous studies have shown that time-averaging of approximately 1000 years is needed to comprehensively sample all species within an 8 km radius of a site, and that fossil richness values increase only slightly with time-averaging greater than 1000 years (Hadly and Maurer 2001).

Taphonomic processes such as those that operated at Porcupine Cave have been shown to reliably sample both presence and relative abundance of most mammals that live within an ~8-18 km radius of the fossil deposit (Hadly 1999; Hadly and Maurer 2001; Porder et al. 2003). The large number of fossil specimens, combined with rarefaction analyses for the Pit Sequence (Barnosky 2004b), further justify our assumption that the fossil deposits adequately sample key aspects of the fossil community, with some caveats that we discuss in more detail below.

Given the likely sampling radius from which the fossil deposits were collected, we estimated the historic sample by counting those mammals whose historic range intersected a circle of 12.5 km radius centered on Porcupine Cave (Fig. 1). By "historic," we mean prior to significant range changes that were caused by European settlers within the last 200 years. The ranges of the historic mammals were taken from maps published by Fitzgerald et al. (1994). This radius seemed the best compromise in view of (a) its being near the midpoint of the probable minimum and maximum radius (8-18 km) from which the fossils were probably collected; (b) the resolution of available maps (Fitzgerald et al. 1994); and (c) the fact that decreasing or increasing the sampling radius by a few km would not substantially change the counts of species.

Taxonomic identifications of fossil material relied primarily on dental and cranial remains, which also are diagnostic in the extant members of the same species or congeners, and are detailed in Barnosky (2004a). The ability to recognize the involved Quaternary species reasonably consistently by using either dental-cranial criteria or soft anatomy (coat color, tail length, etc.) largely mitigates the problem that could potentially arise by comparing the list of historic species (identified largely from soft anatomy) with the list of fossil species. The same higher-level taxonomy was applied consistently to fossil and modern species, following Wilson and Reeder (1993) in most cases (Shabel et al. 2004).

Autecology of the involved species follows standard references (Fitzgerald et al. 1994; Nowak 1999; Wilson and Ruff 1999). Autecological interpretations of fossil species were detailed previously (Shabel et al. 2004). We followed the convention of defining size categories as small (average adult biomass < 0.5 kg), medium (= 0.5-8.0 kg), and large (> 8.0 kg) (Legendre 1986). Lists of taxa recovered from the fossil deposits and the historic sample, with their trophic and size categorization, are given in Appendix 1. We did not include domestic animals in the historic counts (e.g., horses, cows, sheep, domestic cats and dogs, etc.). Neither were shrews nor bats included in the study, because they are not well enough sampled to allow reasonable comparisons between the fossil and historic data sets.

We used chi-square tests to assess the statistical significance of differences between the numbers of fossil and historic species in each trophic and size class, using algorithms in the program JMP IN 5.1 (2002, SAS Institute, Inc., Cary, North Carolina 27513).

RESULTS

Table 1 lists the numbers of species identified in each size and trophic class in the fossil com-

community and in the historic community. The chi-square tests revealed no statistically significant differences between total historic and fossil species richness, or between any of the various pairs of size or trophic categories, with *p*-values for observed differences being due to chance alone ranging from 0.15 to 0.39. However, small numbers of species in some categories reduce the power of statistical comparisons, so to fully explore our data we discuss the largest qualitative differences. Two qualitative differences are obvious — small herbivores are more species-rich in the fossil community (20 versus 13 species), and large omnivores are more diverse in historic time (1 versus 3 species). In all other categories, including the total number of species, the counts are remarkably similar, given that some 850,000 years separates the two communities.

Numbers of species and genera within higher taxa exhibit both similarities and differences between the two time periods (Table 2). Similarities include stable numbers of species in Artiodactyla, and in numbers of genera of Rodentia, Artiodactyla, and all taxa combined. Differences include more fossil rodent species, more fossil lagomorph species and genera, fewer fossil Carnivora, two fossil horse species, and a fossil xenarthran.

For small mammals, which are represented by the most specimens and are therefore probably the most reliably sampled, the numbers of species within genera exhibit considerable stability (Table 3). The biggest difference between the communities of the two time periods is a decrease in the number of vole and lemming species, from nine in the fossil community to four in the historic one.

TABLE 1. Species richness in trophic and size categories for mid-Pleistocene and historic mammal communities in the Porcupine Cave region.

In each column, the number to the left of the colon indicates the number of species in the mid-Pleistocene fossil community, and the number to the right of the colon indicates the number of species present within 12.5 km of Porcupine Cave during historic time (prior to significant European contact). The small and medium herbivore counts for the mid-Pleistocene include the rodents and lagomorphs of Pit Sequence level 4 plus taxa found in the Badger Room. All other counts for the mid-Pleistocene are exclusively from the Badger Room. Small = average adult biomass < 0.5 kg; Medium = 0.5–8.0 kg; Large = > 8.0 kg.

	Size class and trophic group			
	<i>Small</i>	<i>Medium</i>	<i>Large</i>	<i>Total</i>
<i>Herbivores</i>	20 : 13	6 : 7	8 : 7	34 : 27
<i>Carnivores</i>	2 : 3	4 : 4	7 : 7	13 : 14
<i>Omnivores</i>	2 : 2	2 : 3	1 : 3	5 : 8
<i>TOTALS</i>	24 : 18	12 : 14	16 : 17	52 : 49

TABLE 2. Taxonomic richness within orders for species and genera in the mid-Pleistocene and historic communities.

In each column the number to the left of the colon indicates the number of taxa in the mid-Pleistocene fossil community, and the number to the right of the colon indicates the taxa present within 12.5 km of Porcupine Cave during historic time (prior to significant European contact).

<i>Taxon</i>	<i>Species</i>	<i>Genera</i>
Rodentia (rodents)	24 : 20	16 : 16
Carnivora (carnivores)	15 : 19	11 : 13
Artiodactyla (deer, sheep, etc.)	5 : 5	5 : 5
Lagomorpha (rabbits, pikas)	5 : 4	5 : 3
Perissodactyla (horses, etc.)	2 : 0	1 : 0
Xenarthra (sloths)	1 : 0	1 : 0
Primates (humans)	0 : 1	0 : 1
<i>TOTALS</i>	52 : 49	39 : 38

Within higher taxonomic groups, species composition is not stable. Some of the fossil species are extinct congeners of species currently living in the area, and others are extralimital in the sense that they are extant but do not range into our historic sampling radius (Shabel et al. 2004). Overall, about 40% of the species that compose the fossil community are not there today, although in most cases they are represented by functional analogs. For example, whereas the fossil fauna includes an extinct prairie dog species (?*Cynomys andersoni*), an extant congener is found in the historic sample (Barnosky 2004b). Lagomorphs seem to maintain approximately equal numbers of species, but those species are shifted among genera, as illustrated by the counts in Table 2.

DISCUSSION

The difference in small herbivore richness appears to be due, in part, to the fact that a glacial community (the fossil one) is being compared to an interglacial one (the historic sample). Previous work has documented that in this part of Colorado, fewer species of small herbivores are present in the comparatively xeric interglacials than in the more mesic glacials (Barnosky 2004b; Barnosky et al. 2004a). That pattern seems to repeat in the Great Basin where mid-Holocene xeric episodes feature fewer species of small herbivores than more mesic times (Grayson 1998). At Porcupine Cave, the transition from the glacial-age fossil community we analyzed here (that of Pit Sequence level 4) to the superjacent xeric interglacial (Pit levels 3, 2, and 1) that we have reported in previous publications (Barnosky 2004b; Barnosky et al. 2004a) is marked by a drop in small herbivore richness from 20 to 16 species, compared to the 13 species present in historic time. Three of the small herbivore species lost at this time were voles (*Allophaiomys*, *Phenacomys gryci*, *Mimomys*), and one is a pocket gopher (*Thomomys*) — all are taxa that prefer relatively mesic microhabitats (Fitzgerald et al. 1994; Hadly 1999; Wilson and Ruff 1999). On this basis we infer that climatic events such as glacial-interglacial transitions cause numbers of small herbivores to fluctuate, but that the number of species that characterize similar climatic intervals are not dramatically different. Climatic effects on the geographic ranges of small herbivores have been widely reported for other glacial-interglacial transitions as well (Graham and Grimm 1990).

Some of the other differences in small and medium herbivore counts can also be explained by the fact that we are comparing a fossil glacial with a historic interglacial. In interglacial mid-Pleistocene levels of Porcupine Cave (Barnosky 2004b; Barnosky et al. 2004a), the count for overall numbers of Rodentia and Lagomorpha are 20 and 4, respectively, as they are for the historic sample. Within genera or families, the ancient and historic tallies for *Thomomys* and leporids reach parity when the mid-Pleistocene interglacial samples are used (Barnosky 2004b; Barnosky et al. 2004a).

A second possibility for enhanced mid-Pleistocene species richness of small herbivores is that time-averaging has inflated the species count. Whereas the modern counts are based on a temporal snapshot that encompasses less than a century, the fossil counts are based on samples that accumulated over hundreds or perhaps a few thousand years.

In view of these two confounding factors (comparing a glacial with an interglacial, and the potential for time-averaging to inflate our estimates), it is difficult to confidently interpret the differences between the counts in fossil and modern species of small herbivores. However, our conservative assessment is that there are fewer small herbivore species in the historic sample, and that it is in this size category that most fluctuation takes place in species numbers through time, largely in response to climatic fluctuations. Species of arvicolines and *Neotoma* account for most of the reduction (Barnosky 2004b; Barnosky et al. 2004a; and Table 3).

Counts for fossil Carnivora are very likely too low because of sampling considerations.

Carnivorans (especially large-bodied species) typically occur in low abundance in living communities, and unless they utilize caves as dens or hibernacula, their chances of preservation in places like Porcupine Cave are further reduced. That these effects may depress the fossil carnivoran counts in the Badger Room and Pit is illustrated by the situation for bears (ursids). Two species of *Ursus* are present in the historic sample, whereas no ursids occur in the fossil sample from the Badger Room or the Pit Sequence. However, ursids are known from other localities in Porcupine Cave (Barnosky 2004a; Barnosky et al. 2004a), suggesting that they could have been present in South Park at the time the Badger Room and Pit samples were accumulating. This would close the gap between the fossil and historic carnivoran sample. The only other historically present carnivoran lacking in the fossil sample is the raccoon (a procyonid). Members of this family tend to be rare in the fossil record, and it is unclear whether their absence from the fossil fauna from Porcupine Cave is biologically meaningful, or if it is a sampling artifact.

These taphonomic considerations suggest that the gap in species richness between the fossil and historic communities may be even narrower than Table 1 indicates. In the large omnivore category, humans are counted in the historic sample, which we considered valid in view of Native American use of the landscape. Others might argue that humans should not be included in the overall mammal tally. Deleting humans would make the historic and fossil counts closer.

A fluctuation in species richness that may be obscured by the nature of our data is the end-Pleistocene extinction of very large mammals (those > 44 kg) (Martin and Klein 1984; Barnosky 1989; Alroy 1999; Grayson and Meltzer 2003; Barnosky et al. 2004a,b). Our sample is from a time at least 800,000 years before the end-Pleistocene event, and includes at least four species that disappeared from North America at the end of the Pleistocene: the two species of horse, the peccary, and the xenarthran (Table 2 and Appendix 1). A species of mammoth (*Mammuthus*) was not present in our sample (perhaps for taphonomic reasons) but was present in Colorado at the end-Pleistocene (FAUNMAP Working Group 1994). Elsewhere, we (Barnosky 1989; Barnosky et al. 2004b) and many others (Martin and Klein 1984; Alroy 1999; Martin and Steadman 1999; Alroy

TABLE 3. Species richness within genera of small mammals in mid-Pleistocene and historic mammal communities in the Porcupine Cave region.

The mid-Pleistocene list is a composite of the Badger Room and Pit level 4 localities, and the historic list represents the taxa that were reported within a 12.5-km radius of Porcupine Cave during historic time (prior to significant European contact).

<i>Taxon</i>	<i>mid-Pleistocene</i>	<i>Historic</i>
Ochotonids (pika)	1	1
Leporids (rabbit)	4	3
Marmota (marmot)	1	1
<i>Spermophilus</i> (ground squirrel)	2	3
<i>Cynomys</i> (prairie dog)	2	1
<i>Tamiasciurus</i> (red squirrel)	1	1
<i>Tamias</i> (chipmunk)	1	2
<i>Sciurus</i> (gray squirrel)	0	1
<i>Thomomys</i> (pocket gopher)	2	1
<i>Neotoma</i> (wood rat)	3	1
<i>Peromyscus</i> (deer mouse)	1	1
Arvicolines (voles, lemmings)	9	4
<i>Ondatra</i> (muskrat)	1	1
<i>Zapus</i> (jumping mouse)	0	1
<i>Erethizon</i> (porcupine)	1	1
<i>Castor</i> (beaver)	0	1
TOTALS	29	24

2001) have argued that humans influenced species richness at the end of the Pleistocene in North America through interactions with megafauna such that many large-bodied species were deleted from communities. The absence of horses and sloths from around Porcupine Cave may well reflect this end-Pleistocene effect. If so, it is striking that compensations since the Late Pleistocene have resulted in a net loss of only one large herbivore species in historic time relative to the mid-Pleistocene fossil sample. If mammoths were present and not sampled in the mid-Pleistocene, this net loss of large herbivores would climb to two species, and a more striking community difference would be evident in the total absence of elephant-sized species historically.

CONCLUSIONS

When we account for the biases intrinsic to the fossil record, we find surprisingly little difference in overall species richness, or in species richness within major trophic and size categories, between a mid-Pleistocene mammal community and a historic one in the high elevation environment at South Park, Colorado. Total numbers of species in the two time slices are close (52 and 49, respectively), with the main differences accounted for by a decrease in the number of small herbivore species, which we attribute to the effects of climatic fluctuations, and the loss of one or perhaps two large herbivore species, which may have been related to interactions with human immigrants in the late Pleistocene. In view of the major environmental perturbations — including six glacial-interglacial cycles and the immigration of human hunters — that affected the South Park area in the ~850,000 years since our fossil community lived, the similarity between ancient and historic species richness patterns appears more striking than the differences. These results suggest that in communities like the one we studied, there is long-term stability in overall species richness, and structural similarity in how richness is parsed across broad trophic and size categories. Put another way, even in the face of a series of dramatic environmental changes and the first-time introduction of humans into the ecosystem, the South Park mammal community responded with a change in overall species richness that was at most 10% (and probably closer to 5%).

We do not mean to imply that communities do not change through time — they clearly do. In South Park, these changes included a 40% turnover in the species that were present in the mid-Pleistocene, in addition to the relatively minor adjustments in species richness patterns we noted above. What we do suggest, however, is that in our study area species richness exhibited long-term stability, evidenced by a similar total number of species in the fossil and historic samples, and similarity in numbers of species in trophic and size categories. That species richness is so similar across these trophic and size categories, even though the two communities are separated by some 850,000 years, suggests long-term stability in the functional links between constituent species, even though the species may change through time. By “functional links” we mean the way species in one size and trophic category are connected to those in other trophic and size categories, for example, the number of small herbivore species that are available for consumption by medium size carnivore species. Clearly such links between size and trophic categories can change in many different ways, for example, by one species dropping out and the number of individuals of a different species in that category simultaneously increasing in abundance. However, our data suggest that one way that mammalian communities do not change much through time is by fluctuation in numbers of species within different trophic and size categories. This conception of stability in community structure (not in species composition) is consistent with observations of nestedness through time in montane mammal communities (Hadly and Maurer 2001), fluidity of mammalian species ranges at times of climatic change (Graham and Grimm 1990; FAUNMAP Working Group 1996), and constancy in mammalian species richness in communities through tens, hundreds, and thousands of years (Brown et al. 2001).

If it is true that under natural conditions species richness and community structure remain relatively stable through long periods of time, there are important implications for conservation biology. Species richness could provide a simple yet effective metric for assessing whether the functional properties of communities had been perturbed off of a long-term baseline. For example, in South Park, Colorado, we would interpret future changes in species richness to signal an unusual perturbation to the mammalian community if future overall richness deviated in excess of 10% relative to historic richness, because changes of that magnitude would exceed the differences between the ~850,000-year-old fossil community and the historic one. Particularly informative would be changes in the distribution of species richness among size and trophic categories, as that distribution seemed to have remained relatively stable in the absence of significant human impacts, and changes in it signify modification of functional links between species. Such changes now are taking place in the mammal community around Porcupine Cave, as demonstrated by the reduction of species in the large and medium carnivore categories in the past several decades (Barnosky et al. 2004a). As has been suggested elsewhere (Barnosky et al. 2003), changes in species richness are probably preceded by changes in relative abundance of individuals within species; thus, changes in species richness should be regarded as signs of major ecosystem perturbation, the early signs of which might be detected by detailed monitoring of population sizes and geographic range fluctuations.

We emphasize that our results so far apply only to the specific ecological system that we studied — high-elevation mammal communities in the central Rocky Mountains. However, several of North America's major nature preserves exist in similar settings, for example, Rocky Mountain National Park, the Greater Yellowstone ecosystem, and the Glacier-Waterton ecosystem, all of which are characterized by a core National Park surrounded by National Forest and private lands that are used for ranching, agricultural and silvicultural activities, and ecotourism. Thus, monitoring mammalian species richness in such areas may prove a fruitful exercise.

Other pertinent caveats to our suggestion about the stability of species richness include the sampling issues inherent in making comparisons between the fossil record and historic data, the fact that we have compared only two widely separated time slices, and that we have sorted trophic and size categories into conservatively large bins. In view of these caveats, our observations are offered not as a firm conclusion, but as a suggestion that the metric of species richness, especially as distributed across various size and trophic categories, will prove valuable in assessing the degree to which future perturbations shift communities from a long-term functional baseline. The ideas we put forth here can be fruitfully tested by comparing species richness patterns in fossil communities with historic and modern ones in a variety of ecological settings, where sampling issues have been treated appropriately. We note that this approach has been applied with success to both vertebrate (Hadly 1996; Hadly and Maurer 2001; Hadly 2003; Hadly et al. 2003) and invertebrate communities (Tang 2001; Jablonski et al. 2003; Alin and Cohen 2004), and suggest that it can provide a valuable merger between paleontologists, ecologists, and conservation biologists.

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APPENDIX

LIST OF FOSSIL AND MODERN SPECIES USED IN THIS ANALYSIS,
SORTED INTO SIZE AND TROPHIC CATEGORIES.

Small and medium herbivore count for mid-Pleistocene includes rodents and lagomorphs of Pit Sequence level 4 plus taxa found in the Badger Room; all other counts for mid-Pleistocene are exclusively from the Badger Room. Small = average adult biomass < 0.5 kg; Medium = 0.5–8.0 kg; Large = > 8.0 kg. In the right column, where two different English names apply to the same row, the English name for the mid-Pleistocene taxon is given to the left of the comma, and the name for the historic taxon appears to the right of the comma.

<i>Mid-Pleistocene</i>	<i>Historic 12.5 km radius</i>	<i>English name(s)</i>
Large carnivores		
<i>Canis</i> sp. "small canid" †		Small canid sp.
<i>Canis latrans</i>	<i>Canis latrans</i>	Coyote
<i>Canis edwardii</i> †	<i>Canis lupus</i> **	Edward's wolf, Gray wolf
<i>Lynx rufus</i>	<i>Lynx rufus</i>	Bobcat
	<i>Lynx lynx</i> **	Lynx
<i>Taxidea taxus</i>	<i>Taxidea taxus</i>	American badger
<i>Miracinonyx</i> cf. <i>M. inexpectatus</i> †	<i>Felis concolor</i>	Irvingtonian cheetah, Puma
Lutrinae, indet. †	<i>Gulo gulo</i> **	Otter, Wolverine
Medium carnivores		
<i>Mustela nigripes</i>	<i>Mustela nigripes</i> **	Black-footed ferret
<i>Mustela</i> sp. nov. †	<i>Mustela vison</i>	Mustelid sp. nov., American mink
<i>Martes diluviana</i> †	<i>Martes americana</i>	Extinct fisher, American marten
<i>Vulpes vulpes</i>	<i>Vulpes vulpes</i>	Red fox
Small carnivores		
<i>Spilogale putorius</i>	<i>Spilogale gracilis</i>	Eastern and Western spotted skunks
<i>Mustela frenata</i>	<i>Mustela frenata</i>	Long-tailed weasel
	<i>Mustela erminea</i>	Ermine
Large herbivores		
<i>Erethizon dorsatum</i>	<i>Erethizon dorsatum</i>	Porcupine
<i>Antilocapra/Tetrameryx</i>	<i>Antilocapra americana</i>	Pronghorn spp.
Antilocapridae, indet.	<i>Odocoileus hemionus</i>	Pronghorn indet., White-tailed deer
<i>Equus</i> sp. "small" †	<i>Cervus elaphus</i>	Small horse, Elk
<i>Equus</i> sp. "large" †	<i>Bison bison</i> **	Large horse, Bison
Ovibovini, indet.	<i>Ovis canadensis</i> **	Muskox sp., Bighorn sheep
<i>Ovis</i> sp. †	<i>Castor canadensis</i>	Sheep sp., Beaver
<i>Paramylodon harlani</i> †		Ground sloth
Medium herbivores		
<i>Ondatra amnecens</i> †	<i>Ondatra zibethicus</i>	Extinct muskrat, Extant muskrat
<i>Marmota</i> sp.	<i>Marmota flaviventris</i>	Marmot sp., Yellow-bellied marmot
<i>Cynomys</i> cf. <i>C. leucurus</i> *	<i>Cynomys gunnisoni</i>	Prairie dog sp., Gunnison's prairie dog

	<i>Sciurus aberti</i>	Abert's squirrel
<i>Lepus</i> sp.	<i>Lepus townsendii</i>	Jackrabbit sp., White-tailed jackrabbit
<i>Sylvilagus</i> sp.	<i>Sylvilagus nuttallii</i>	Cottontail sp., Mountain cottontail
<i>Azlanolagus</i> sp. †	<i>Lepus americanus</i>	Aztlan rabbit, Snowshoe hare
Small herbivores		
<i>Spermophilus</i> cf. <i>S. elegans</i> †	<i>Spermophilus elegans</i>	Wyoming ground squirrel
? <i>Cynomys andersoni</i> , sp. nov. †	<i>Spermophilus tridecemlineatus</i>	Prairie dog, Ground squirrel
<i>Tamiasciurus hudsonicus</i> *	<i>Tamiasciurus hudsonicus</i>	Red squirrel
<i>Tamias</i> cf. <i>T. minimus</i> *	<i>Tamias minimus</i>	Chipmunk sp., Least chipmunk
	<i>Tamias quadrivittatus</i>	Colorado chipmunk
		Extinct vole
<i>Allophaiomys pliocaenicus</i> †		
<i>Phenacomys gryci</i> †	<i>Clethrionomys gapperi</i>	Gryci's vole, Southern red-backed vole
<i>Phenacomys</i> sp. (not gryci)*	<i>Phenacomys intermedius</i>	Western heather vole
<i>Microtus paroperarius</i> * †	<i>Microtus longicaudus</i>	Extinct microtus, Long-tailed vole
<i>Microtus meadeensis</i> * †	<i>Microtus pennsylvanicus</i>	Extinct microtus, Meadow vole
<i>Microtus</i> "5T form" †		"5T" vole
<i>Mimomys virginianus</i> †		Virginia mimomys
<i>Lenmuisus</i> sp.*		Sagebrush vole sp.
<i>Mictomys kansasensis/meltoni</i> †		Bog lemming sp.
<i>Neotoma cinerea</i>	<i>Neotoma cinerea</i>	Bushy-tailed woodrat
<i>Neotoma floridana</i> *		Eastern woodrat
<i>Neotoma micropus</i> *		Southern plains woodrat
<i>Brachylagus</i> sp.		Pygmy rabbit sp.
<i>Ochotona</i> cf. <i>O. princeps</i>	<i>Ochotona princeps</i>	Pika sp., American pika
<i>Thomomys</i> sp.	<i>Thomomys talpoides</i>	Pocket gophers
<i>Thomomys</i> cf. <i>T. bottae</i> *		Pocket gopher sp.
	<i>Zapus princeps</i>	Western jumping mouse
Small omnivores		
<i>Spermophilus lateralis</i>	<i>Spermophilus lateralis</i>	Golden-mantled ground squirrel
<i>Peromyscus</i> sp.	<i>Peromyscus maniculatus</i>	Deer mice
Medium omnivores		
<i>Mephitis mephitis</i>	<i>Mephitis mephitis</i>	Striped skunk
<i>Brachyprotoma obtusata</i> †	<i>Bassariscus astutus</i>	Short-faced skunk, Ringtail
	<i>Procyon lotor</i>	Raccoon
Large omnivores		
<i>Platygonus</i> sp. †	<i>Ursus americanus</i>	Peccary, American black bear
	<i>Ursus arctos</i> **	Brown bear
	<i>Homo sapiens</i>	Human
Small insectivores		
<i>Sorex</i> sp.	<i>Sorex</i> spp.	Shrews
<i>Chiroptera</i> , indet.	<i>Chiroptera</i> spp.	Bats

* = added from Pit Level 4 ** = extirpated since Historic † = extinct

Species Numbers in Bacteria

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A modified biological species definition (BSD), i.e., that bacteria exchange genes within a species, but not usually between species, is shown to apply to bacteria. The formal definition of bacterial species, which is more conservative than the modified BSD, is framed in terms of DNA hybridization. From this I estimate there are a million species of bacteria in 30 grams of rich forest topsoil and propose that there will be at least a billion species worldwide.

Bacteria are a major component of the cellular life on Earth and are found everywhere from the top of mountains in Antarctica to the deep-sea vents. They are found in the deep subsoil, the open ocean and all over every surface of you. The refrain for undergraduates is that only about 10 percent of the cells moving with you are eukaryotic, the rest bacterial symbiotes. But because bacterial cells are so much smaller than eukaryotic cells, they make up only about 10 percent of your weight. (So, tomorrow, when you step on the scale you can subtract 10 percent off the scale weight because it is not really yours.)

Of the three great branches of cellular life, two are bacterial: the Eubacteria and the Archeae. The third branch is the Eukaryotes of which plants, animals, and fungi make up three kingdoms. The Eubacteria are divided into 40 kingdoms and the Archeae are divided into two kingdoms. The question I will try to answer in this paper is how many species of bacteria might there be. Before we can estimate the number of species of bacteria there may be in the world, we have to determine whether bacterial species are real entities and how they can be defined.

BACTERIAL SPECIES

Bacteria are different from eukaryotes in an essential characteristic of life history. Bacteria are haploid and always reproduce asexually by fission. They have other mechanisms for sex, the transfer of genes between lineages, such as transformation, transduction, and conjugation.

The effects of sex in bacteria are different than in animals. In bacteria only a small fraction of the genome is transferred, unlike animals, where 50% of the offspring genome is transferred from the male during sex. Sex in bacteria can be between clones of the same species, closely related species, or distantly related species, whereas in animals sex is almost always limited to members of the same species. During sex in bacteria, pieces of genes or whole genes are transferred and replace the alleles present by homologous recombination, rather than form heterozygotes of the female and male alleles as in animals. Also, in bacteria, new genes can be added to the genome by non-homologous recombination.

The distinction between sexual and asexual as is made in plants and animals does not make sense for bacteria. The amount of sex, or lateral gene transfer between lineages, in bacteria can vary from very little to a lot. *Borrelia burgdorferi*, the causative agent of Lyme disease, is almost com-

pletely clonal, only transferring small pieces of DNA very rarely (Dykhuizen and Baranton 2001). In *Helicobacter pylori* (Suerbaum et al. 1998), the causative agent of stomach ulcers, and *Neisseria gonorrhoeae* (O'Rourke and Spratt 1994), the causative agent of gonorrhea, there is so much sex that alleles of different genes are in linkage equilibrium.

There is a certain flexibility in the bacterial genome as to what genes are present, even within a species. This part, which ranges from zero to about 20 percent of the genome (Ochman et al. 2000; Daubin et al. 2003a), is represented by genes that are transferred into the cell by non-homologous recombination and are fairly readily lost again. Belonging to this class of genes are DNA parasites like insertion sequences, transposons, lysogenic phage, small plasmids, and probably restriction modification systems. There are also genes that are involved in local adaptation to particular environments such as the genes in pathogenicity islands, antibiotic resistance genes in plasmids (mini chromosomes), genes for resistance to toxins and heavy metals, and genes and operons for various specialized functions. Generally, the genes in this pool of transients are either DNA parasites or genes that are locally adapted (Eberhard 1990). The genes that are generally useful to the organism across all the environments in which it lives are found in all strains and are usually associated with the major chromosome. Some of these genes are particular to a species or a small group of species, but most are widely found throughout bacteria. These genes, such as those involved in protein synthesis, DNA metabolism, energy generation and usage, etc., are often called housekeeping genes.

Some individuals (e.g., Gogarten et al. 2002) have been so enamored by this novel aspect of bacteria, the rapid and possibly widespread transfer of DNA across species, that they have suggested bacterial cells are simply holding vessels for the genetic variation available in the bacterial gene pool. The part of this pool seen in any particular cluster (species?) is simply the genes that are selectively useful given the current environment. Thus, bacterial phylogeny would represent ecology more than history.

I do not think this is true, but rather bacterial species can be defined in ways that are very similar to the way animal species are defined. I proposed in 1991 that bacterial species could be defined as a variant of the biological species definition (Dykhuizen and Green 1991). To restate and update that definition, I will define a species as a group of individuals where the observed lateral gene transfer within the group is much greater than the transfer between groups such that phylogenetic history is preserved when genomes are compared. Below I will illustrate what I mean by this definition. But before this, I want to make two comments. The first is that I think the similarity between species in bacteria and in animals occurs because species are real and caused by the same basic biology in both cases. Although it is still not clear what this basic biology is, just as it was not clear what basic biology the Linnaean hierarchical system of classification described before Darwin's theory of descent, I will present my idea of what this basic biology is later. The second involves the idea of "observed transfer" in the definition. The rates of observed transfer will depend upon both the rate of transfer and the selection for or against the strains containing these transfers. Generally, the rates of transfer will decrease with phylogenetic distance (Majewski and Cohan 1998) and the selection against the transferred DNA will increase with phylogenetic distance (Cohan et al. 1994), such that transfer is seen within species but not between species (see below). Of course, if the environment changes, as, for example, humans using tremendous amounts of antibiotics for the health and growth of themselves and their animals, even rare transfers of DNA from phylogenetically distance sources will be strongly selected if they provide resistance. The ability to incorporate DNA from outside the species is an advantage that generally distinguishes bacteria from animals. In animals and plants, incorporation of DNA from different taxa is unlikely, but can happen when associated with endosymbiosis.

The first example supporting a BSD involves *Escherichia coli* and *Salmonella*. It is well established that there is recombination between strains of *E. coli* (Dykhuizen and Green 1991; Guttman and Dykhuizen 1994). However, there is also evidence that there is little or no transfer between *E. coli* and *Salmonella* and none from more distantly related bacterial species into either of these two closely related species. Because this is not generally realized, I will describe the evidence in detail. Figure 1 shows the sequence distance between homologous genes of these two species plotted by a measure of codon bias (Sharp 1991). Codon bias refers to preferential use of certain codons over others even though all the codons code for the same amino acid. Highly used genes show more bias than less used genes. Highly used genes synthesize more protein, placing a larger demand upon the pools of charged tRNA. The preferred codons are the codons for tRNA types with the largest pools and the unpreferred codons are the ones with the smallest pools of tRNA. Thus, there is selection to use the preferred codons, which is stronger in highly used genes. Because the codon preference in *E. coli* and *Salmonella* is the same, genes with high codon bias will diverge less rapidly than ones with low codon bias (Fig. 1).

Like the dog that did not bark, Figure 1 is very clear in what it does not show. There are no points in the upper right and lower left sections (except the four open circles). If a gene had been transferred into either species from a more distantly related species, the distance between *E. coli* and the *Salmonella* copies would be much greater than expected for amount of codon bias seen. If there had been a recent transfer between *E. coli* and *Salmonella*, the gene copy that had been evolving in one species since the separation of the two species would be replaced by one from the other species and the distance would be too small given the codon bias. The circles in the figure are noted by the author as having too small a distance given the bias and are possible cases of lateral gene transfer between the species. However, he suggests that for the three open circles on the left, the mutation rate is lower because these genes are contiguous and near the origin, giving a smaller than expected distance, rather than these genes having transferred between the species well after the species split. This supposition has been strongly supported (Ochman 2003). The open circle on the right represents the *tufA* and *tufB* genes. These are very highly synthesized genes, expected to have strong codon bias. The position and phylogeny of the duplications make it very unlikely that the small distance was caused by recent lateral transfer rather than strong selective constraint (Sharp 1991). In conclusion, although there is strong evidence that there is recombination between lineages for housekeeping genes within *E. coli*, there is no evidence of gene transfer between *E. coli* and *Salmonella*. Thus, we can consider these as two distinct species by my definition of species. Using whole genome sequences, Daubin and collaborators (2003b) have shown recombination within *Escherichia coli* and *Chlamydomophila pneumoniae*, but lack of recombination between at least seven species. Thus, it seems that my definition of species will be robust.

Salmonella enterica has been thought to have very limited recombinational exchange (Feil et

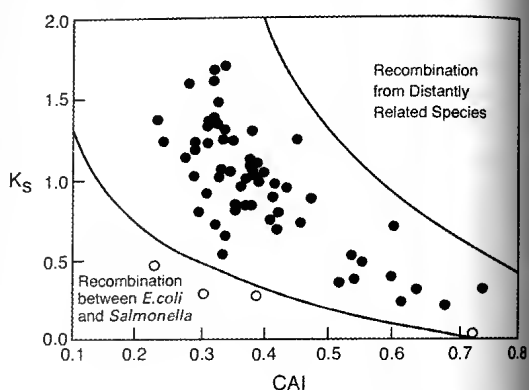


FIGURE 1. Plot of codon bias by sequence divergence between genes found in *E. coli* and *Salmonella*. CAI (Codon Adaptation Index) is a measure of codon bias. K_s is the number of substitutions per synonymous sites, where the distance is corrected for multiple hits using the Kimura two-parameter model (Kimura 1980). This figure is modified from Figure 1 of Sharp 1991. Codon bias explains 50% of the variation in synonymous site divergence. The open circles are the genes that might have been laterally transferred after the species split.

al. 2001, Maynard Smith 1995). This conclusion was based upon studying two examples of each of eight subspecies. To show recombination within a taxon, one needs at least three individuals. Thus, this test could not determine recombination within the subspecies. Brown et al. (2003) recently have shown that there is extensive recombination within one of the subspecies. Thus, the conclusion is that *Salmonella enterica* is likely to be eight separate species.

We suggested that if there is no genetic exchange between species, then all the gene trees should be congruent (Dykhuizen and Green 1991). Lawrence et al. (1991) showed gene tree congruence for three genes across a number of species in enterobacteria. More recently this work has been extended using whole genomes (Lerat et al. 2003). They found concordance for 203 out of 205 gene trees across 11 species. The two exceptions were inconsistent because of a single lateral gene transfer (LGT) event. The conclusion of Lerat et al. (2003) very strongly supports our definition of bacterial species: "Our analysis indicates that single-copy orthologous genes are resistant to horizontal transfer, even in bacterial groups subject to high rates of LGT" (p. 101).

The *Neisseria* are a group of species that are primarily commensals of the mucous membranes of mammals. There are a group of seven species that are commonly found associated with humans, six of which are found in the back of the mouth and the seventh, *N. gonorrhoeae*, in the urogenital tract. These bacteria are naturally competent for transformation throughout their entire life cycle and have high rate of LGT (Spratt et al. 1995). *N. meningitidis* and *N. gonorrhoeae* are closely related, with the DNA of coding genes >98% sequence identity. Although there is extensive genetic exchange within each species (Maynard Smith et al. 1993), there is little exchange between them (Vazquez et al. 1993), conforming to the Biological Species definition. This is presumably because they are physically isolated, living in different parts of the body. The six species living in the throat do exchange DNA even though they are more distantly related with sequence similarity among species ranging from 91% to 77%. Because of strong selection, pieces of the gene for the penicillin binding protein from two of the naturally penicillin resistant species have been incorporated into *N. meningitidis*, rendering it resistant to penicillin, even though the divergence is 14% for one species and 23% for the other (Spratt et al. 1995). Clearly, strong selection can incorporate genetic material from other species into the genome. However, what happens when there is no strong selection? When housekeeping genes are sequenced from these species, fragments from other species are present in many of the genes. These fragments are recent transfers that have not yet been purged by selection, because when the fragments are removed, the gene trees generally match (Maynard Smith 1995). If fragments had been incorporated in the past, the gene trees would not match. Thus, the fragments must have been selected against.

This is proven by an exception. The *adk* gene is scrambled (Feil et al. 1995). Why do we see extensive recombination in this gene and not in others? I think the answer is that *adk* has only one polymorphic amino acid across the genus whereas the other genes have many. Thus, I conclude that there is selection against fragments from other species because of amino-acid differences, i.e., the genome is co-adapted. This maintains species boundaries. Because of this general property of cellular life, the co-adapted gene complex, species definitions can be very similar for bacteria, animals and plants.

NUMBER OF SPECIES IN 30 GRAMS OF SOIL

Whereas there are many species definitions (e.g., Cohan 2002), I wish to use the formal definition of species in bacteria because it is both useful and conservative. It states, "The phylogenetic definition of species generally would include strains with approximately 70% or greater DNA-DNA relatedness and with 5°C or less Δt_m . Both units must be considered" (Wayne et al.

1987:463). Thus two strains are different species if less than 70% of the DNA will re-associate after having been melted to single strands. This criterion is required because up to about 30% of the DNA of a bacterial cell can be transient. Also, mismatches will decrease melting temperature of the re-associated DNA. For two strains to be different species, this decrease must be more than 5°C. This translates to 7–8% difference in DNA sequence (Caccone et al. 1988). Thus, by this conservative definition, *N. gonorrhoeae* and *N. meningitidis* would be considered the same species.

We can use this definition to estimate the number of bacterial species in a community. The rate of re-association of single stranded DNA with its homologue depends upon the concentration of the homologue. As the number of different fragments of DNA increases, the time becomes longer. Figure 2 shows the re-association of *E. coli* DNA and calf thymus DNA. The genome of a calf is larger than the genome of *E. coli*, consequently it takes much longer for the calf thymus DNA to re-associate than the *E. coli*. Re-association kinetics are measured in terms of the concentration of DNA in moles per liter (C_0) times the time in seconds (t). This is the Cot value. If the concentration of DNA is held constant, then the number of molecules of each unique sequence decreases as the genome size increases. For example, if the concentration of DNA is 12pg, a solution will contain 4000 copies of a genome of 0.003pg but only 4 copies of a genome of 3pg. In this example it will take on average 1000 times longer for the DNA in the large genome to find its homologue. The Cot value, when half the DNA is re-associated, gives an estimate of genome size. If we think of the bacteria from a natural community as a single species of bacteria, how large would its "genome" be? The number of species in the community can be estimated by dividing this "genome" by the average size of a bacterial genome.

Torsvik, Goksøyr and Dane (1990a) isolated 30 grams of top-soil from a beech forest north of Bergen, Norway. The soil contained 1.5×10^{10} bacteria per gram by microscopic observation. Less than 1% of these could be cultivated. After the eukaryotes and viruses were eliminated, DNA was extracted from the bacteria. The DNA was sheared, melted, and allowed to re-associate at a temperature that was 25°C less than the melt temperature. As seen in Figure 2, the re-association started at about the same time as the calf thymus DNA, which implies that the most common species is less than 1% of the population. The re-association at 50 percent is 10 times more complex than the calf thymus DNA. This gives an estimated complexity of 2.7×10^{10} bp. If you take the average genome size of soil bacteria at 6.8×10^6 bp (Torsvik et al. 1990b), which is a little larger than *E. coli*, you end up with an estimate of about 4000 common species. The rare species have still not re-hybridized. Actually the 4000 is an underestimate, because the re-association is 25 degrees below the melt temperature. If this re-associated DNA is melted, only 10 percent of the re-associated DNA fits within the definition of species (a Δt_m of less than 5°C). This suggests that we have underestimated the number of

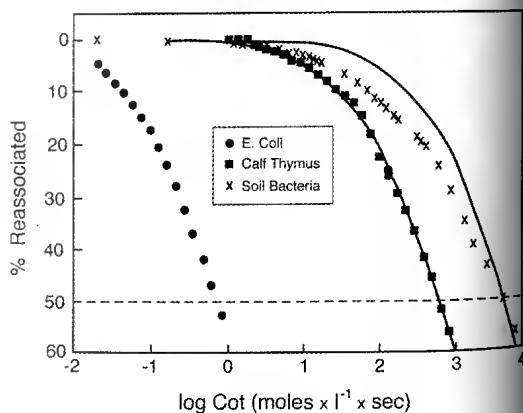


FIGURE 2. DNA rehybridization kinetics. This figure is a modification of Figure 3 of Torsvik, et al. (1990a). The *E. coli* genome is about 4.5 megabases and the unique DNA in cows is about 1,000 times larger as is human. Thus the initial hybridization of the soil bacterial DNA at same point that the calf thymus starts to re-hybridize suggests that the most common species in the soil is about one tenth of one percent of the total number. The line at the far right is the re-association kinetics for a homogenous sample like the calf thymus DNA, shifted so it has the same Cot as the soil bacteria at 50% re-association. This shows that the different species of DNA from the soil have very different frequencies.

species by ten fold. Using strains isolated from the soil, Torvick et al. (1990b) showed that the DNA hybridization gave a number of species ten-fold too low. So we end up with 40,000 common species.

There are always fewer common species than rare ones. If the species are ranked by number of individuals so that the most common species is first and the rarest species is last, then we can divide the species into two classes, each containing half the individuals in the sample. The ratio of the number of rare species to the number of common species gives us an estimate of the total number of species when we can only estimate the number of common species. Consider an example with 52 species. The two most common species make up half the number of individuals. Then the ratio of rare species to common species is 25 to 1. This is about average ratio found in the literature for animals and plants (Dykhuizen 1998). The ratio estimated from the data of Ruth Patrick (1968) on natural communities of diatoms is 25 if we use only the data from a single experimental box, but 35 if we combine the data from all eight boxes. Thus, as a first approximation, we will use a ratio of 25 to estimate the number of species in 30 grams of soil. This is 25 times 40,000 or a million species. There are caveats to this estimation. For example, a lot of the rarity might be in rare genes that are laterally transferring back and forth rather than in rare species. Thus, we need another way of estimating the number of species in this 30 grams of soil. This is provided by the work of Curtis and collaborators (2002).

Curtis et al. (2002) proposed using log normal species abundance curves to characterize bacterial communities. If the total number of bacteria and the number of the most common species are known and if it is assumed that the rarest species is present as a single individual, then the total number of species can be estimated. There are 5×10^{11} bacteria in 30 grams of soil and the most common species is between 1% and 0.1% of this number. Reading off Figure 4 of Curtis et al. (2002), the possible values for the numbers of the most common species give an estimate that span the value of a million species in this 30 grams of soil.

THE NUMBER OF BACTERIAL SPECIES IN THE WORLD

We know very little about how many communities of bacteria there are and what the diversity may be within them. Although there may be a million bacterial species in 30 grams of rich soil in Norway, this might be one of the more diverse communities because it is in a nutritionally rich, structured and stable environment. I would expect similar soils (where I do not know what I mean by "similar") to have the same species, such that the number of species present in this type of soil worldwide would be about ten million in 3000 kilograms of soil (Curtis et al. 2002). The bacterial communities in sandy loam, sandy clay loam, loamy sand, and clay loam in England were tested by DNA-DNA hybridization and found to be different (Griffiths et al. 1996). There is some cross-hybridization between certain soil types. When there is some cross-hybridization, is this because the communities contain the same species in very different densities or is it because some of the species are shared between the communities, but most are different? Another way of asking this question is: "Are the rare species in one environment, common in another or are rare species rare and common species common?" The data of Patrick (1968) for a number of communities of protists in very similar experimental environments suggests the latter is true. Finley et al. (2002) suggests it is true for fresh-water protists. This might not be true of diatoms because the environment in the ocean is not structured as in soil and freshwater lakes. However, I will assume it is also true for bacteria, i.e., rare species are rare and common, common, even in different soil types. Thus, the different soil types are likely to represent different communities of bacteria. How many soil types are there in the world that support different communities of bacteria? Do different plants on

the same soil type give different communities? We will need more data to answer these questions to be able to estimate how many species of soil bacteria there are in the world.

Curtis et al. (2002) suggested there are about two million species in the ocean. This is derived from estimating there are 163 species in a ml of seawater from the Sargasso Sea and then extrapolating this to two million in the ocean. However, the Sargasso Sea has very different bacterial community than Long Island Sound (Lee and Fuhrman 1990). Even within the Sargasso Sea, the communities at the surface and at 500 meters are different (Lee and Fuhrman 1990). Whereas there is no cross-hybridization between the Sargasso Sea and Long Island sound, there was some for the different communities at the surface and at 500 meters. Once again, is there cross-hybridization because the same species are present at the two depths, but in different ratios, or is there some species overlap, giving some cross-hybridization, but with most of the species different? If we assume the latter, then the estimate of Curtis et al. (2002) is probably a considerable underestimate.

In this symposium, Nancy Knowlton mentioned the large diversity of bacteria on corals and presented evidence for species specificity (Rohwer et al. 2002). We also know there is a community of bacteria in the deep sub-soils. Even at 500 m, the U.S. Department of Energy continues to find bacteria in their deep wells. Antarctic rocks contain bacteria that only metabolize three or four hours a year when the sun is directly on them; otherwise they are frozen. There are bacteria everywhere. Thus there must be many communities and consequently very many species.

From all this, my guess is there are a billion species and the more I get used to this number, the more I feel it is a gross underestimate. But for now, it is as far as my mind will go, given so little data. Thus, there are simply too many species of bacteria to count. Returning to Paul Ehrlich's argument, we need other measures of biodiversity, particularly for bacterial communities, than sampling and counting every species. Perhaps we can use DNA re-association measures or some method involving PCR to get estimates of the diversity. These measures can be used over time to look at community stability and ecosystem health. In an aside, it seems that PCR amplification directly from bacterial communities, sequencing these PCR products and estimating species number using rarification statistics from these sequences underestimates species diversity by about ten-fold.

QUESTIONS AND ANSWERS

How Many Named Species of Bacteria are There?

There are about 30,000 formally named species that are in pure culture and for which the physiology has been investigated. Species now are being defined by PCR amplifying ribosomal genes and sequencing. The criterion for defining species is that the ribosomal genes are at least 3% different. This method is probably even more conservative than DNA/DNA re-association methods for defining species. We're probably defining species by ribosomal sequence at the level of genera or family.

What is Known About the Distribution of Bacterial Species Around the World?

Almost nothing. We know something about the biogeography of infectious diseases. Many of them are worldwide with very little population differentiation, like *E. coli*. Some of them are very specific to particular regions. So for example, the spirochete that causes Lyme disease is mostly found on the coastal plane of the east coast of the United States from the islands off Maine down to Maryland, and in the region of central Wisconsin, southern Minnesota and into the upper peninsula of Michigan. There is also a region in the central valley of California. There are low densities

of this spirochete in other areas, but it seems that the biotic cycle in these regions prevents high densities of both ticks and Lyme disease. Particularly along the northeast coast of the United States, it seems that the high density of Lyme disease matches the region of the last major glaciation. This correlation is probably because of the lower biodiversity (particularly of reptiles) after the glaciation. I must add one thing. The bacterial ecologists have a motto, which I don't think is completely correct, but does have some bearing. The motto is that is that everything gets everywhere, it's the environment that counts. So you find the same species in Yellowstone as you do in the hot springs in Iceland.

What will Happen as Biodiversity Decreases?

I'm speculating right now, but I think we're going to get more epidemics as biodiversity declines. What will happen is that the other species that are left will go up in numbers, and the organisms that infect them of course will go up in numbers. This means that there is a larger chance for them to jump to humans, which are a vast and untapped resource. We make the oil fields of Iraq look like a minor player as far as energy resources for bacteria go.

How Many Species of Bacteria are Found on Humans?

When I start my classes, I say that the bacteria on you are 90 percent of the cells that you walk around with. Only 10 percent of the cells that you walk around with are you. But they're much smaller. They are only 10 percent of the biomass. So you would only lose 10 percent of your weight if you got rid of all your bacteria. I don't think we really know how many species are found on humans. We're talking about 400-500 in your mouth, around the plaque. It seems that about 100 in your intestinal tract give you normal intestinal functioning. Germ-free mice don't function well. So that's not a very happy answer, but at least we're talking in the hundreds. Many of them are probably unique to humans.

Is Anybody Doing Similar Work Amongst Single Cell Eukaryotic Organisms?

Of this kind of measure within a system I don't think so. Single cell eukaryotic organisms are already much larger than bacteria. There's an attempt to do that picking out individual ones and looking at what species they would fall into. There's a lot of work trying to do the taxonomy of single cell eukaryotes. That's very exciting.

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Mapping Patterns of β — Diversity for Beetles Across the Western Amazon Basin: A Preliminary Case for Improving Inventory Methods and Conservation Strategies

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Beetles sampled by insecticidal fogging were investigated to test for temporal and spatial β -diversity between two western Amazon rain forest sites located less than one-degree latitude from the equator and 21 kilometers distant from each other. A rigorously controlled sampling regime of terrestrial arthropods in the canopy and understory resulted in a dataset containing trans-seasonal and trans-annual information. This paper focuses on the Carabidae and Curculionidae (Otidoccephalini) from a larger dataset because the species accumulation curves for them nearly reaches an asymptote, that is, enough samples have been sorted to account for nearly all the canopy species in the general area. Canopy trees in the two sites are very different at the species level (Complementarity Index = 0.73), moderately different at the generic level (CI = 0.53), but similar at the family level (CI = 0.26). The beetle fauna was predicted to be different at the two sites depending upon feeding guilds because the tree species composition is so different. The assumption is made that plant feeding species have some degree of host specialization, whereas predators and scavengers do not. For otidocephaline Curculionidae and Carabidae, this analysis suggests the opposite of that prediction: a larger percentage of herbivore species are shared between sites than predator species. These results suggest variable degrees of species turnover across short distances in both forest composition and their insect dependents in the western Amazon Basin and this may impact inventory methods and the conservation strategies derived from them.

Se estudiaron coleópteros muestreados con la técnica de fumigación para determinar la tasa de recambio temporal y espacial de especies (diversidad- β) entre dos sitios que corresponden a Bosque Húmedo Tropical, localizados a menos de un grado de latitud de la línea Ecuatorial y 21 kilómetros de distancia entre ellos. Un riguroso muestreo de artrópodos terrestres habitantes del dosel y sotobosque, resultó en un amplio registro de datos conteniendo información inter-estacional e inter-anual. Esta investigación se centra principalmente en las familias Carabidae y Curculionidae (Otidoccephalini) debido a que sus curvas de acumulación de especies casi alcanzan una asíntota, esto significa, que se han tomado suficientes muestras para registrar todas las especies presentes en el área general. Entre los dos sitios, los árboles son muy diferentes a nivel especie (Índice de Complementariedad = 0.73), moderadamente diferentes a nivel de género (IC= 0.53), pero similares a nivel de familia (IC =

0.26). Predecimos que los escarabajos difieren dependiendo de sus gremios tróficos ya que la composición de árboles es diferente. Se asume que las especies herbívoras tienen algún nivel de especialización hacia las plantas huéspedes, mientras que los predadores y carróñenos no. Para los Otidoccephalini y Carabidae, nuestro análisis sugiere lo opuesto a nuestra predicción: encontramos que el porcentaje de especies herbívoras compartidas entre sitios es mayor que el porcentaje de las especies predadoras compartidas. Estos resultados sugieren grados variables en la tasa de recambio de especies a través de distancias cortas tanto a nivel de composición vegetal del bosque como en los insectos asociados en la cuenca Amazónica Occidental, lo cual puede tener un impacto en los métodos de inventario y en las estrategias de conservación derivadas de estos.

Crucial to strategic planning for conservation areas is knowledge of species diversity and their distributions, at both local and regional scales across a multitude of fractal universes. If the goal of conservation strategies is to provide reserved areas for *most* of biodiversity, and that *should* be the goal, knowledge is needed from the fractal universe of mites and tardigrades to that of large trees and their vertebrate inhabitants. Eventually, as technology catches up with inventory, this means that the minute organisms (internal and external parasites, bacteria, viruses, etc.) inside and on the mites and tardigrades will need documentation, as well. However, at present we have no reasonably complete biodiversity map (Wilson 2000) that is valid for more than a miniscule percentage of life on the planet, nor do we have practical technology to access the smallest of species — the prokaryotes. Not even all vertebrates, butterflies, nor tree species are well mapped at scales to be significantly meaningful at a global scale. As pointed out by Lowman and Wittman (1996) and Basset (2001), we know little thus far about patterns in tropical forest canopies, the very heart of biodiversity (Erwin 1988). Thus, the question arises, how does one plan areas for conserving most of the species occurring locally or regionally? Areas now receiving attention may or may not contain the same species, whereas those not attended to may have a substantially different fauna and flora. Assumptions derived from larger and supposedly well-known organisms may not serve at all for minute insects living in the rain forest canopy (*cf.* Carroll and Pearson 1998).

Our investigation was undertaken to determine spatial and temporal turnover (β -diversity) across 21 kilometers distance in tropical lowland rain forest at the equator in the western Amazon Basin (on the margin of Yasuni National Park) with a very large dataset containing trans-seasonal and trans-annual information. By definition, the two sites studied are representatives of the local fauna and flora in a continuous lowland rain forest, but the question remains, how much of the regional forest biodiversity do they actually represent? Such Neotropical forests are complex not only in species composition, but also in forest architecture. Because these equatorial forested sites are complex, it was thought that a study of their canopy and understory arthropod fauna might provide crucial insights regarding the distribution of most of biodiversity in time and space. They were, thus, chosen for intensive long-term biodiversity and taxonomic studies. Several studies have suggested that the western Amazon Basin is the richest biome on Earth (Erwin 1982, 1983a, 1983b, 1988; Lamas et al. 1991; Gentry 1993; Kress et al. 1998; Heyer et al. 1999; and Pitman et al. 2001). Preliminary observations across the western Amazon Basin of one family of a dominant tropical canopy beetle family (Carabidae) indicated that nearly complete species turnover might be occurring every 250 kilometers (*cf.* Lucky et al. 2002). Unfortunately, methods of collecting and sample size were not sufficient to give solid evidence for this pattern. For the most part, carabid beetles are predators. What might be the turnover across distance/seasons for other guilds of beetles? One might predict that scavengers, like predators, would be more widespread, whereas herbivores and other types of feeding specialists would be more restricted. In addition, one might predict that host

restricted herbivores and fungivores would have a similar pattern to their hosts locally, but what about co-occurring regional patterns? Do local patterns hold regionally? This investigation opens exploration of some of these questions and predictions with canopy and understory fogging events (Erwin 1989; Lucky et al. 2002) on the equator in the western Amazon Basin.

Here, we initiate our reports stemming from fogging events at each of two localities resulting in more than 500,000 beetle specimens. This initial paper focuses on our methods, sites, suite of study taxa, particularly beetles of two families, and observations from preliminary data of another 14 family-group taxa. We regard our 16 family-group taxa as a first cut into the massive amount of data collected over eight years of field work at four month intervals over an eight year period. Processing 1800 samples containing one half million specimens and taking them to an identification level of morphospecies are not easy chores. However, we believe that by reporting on our studies periodically we will provoke debate and interest in the project. Our subsequent investigations will include as many feeding guilds and phylogenetic lineages as possible.

FIELD SITES AND METHODS

Data for the beetles and site vegetation reported in our investigation came from a canopy arthropod biodiversity study, conducted at Onkone Gare Station (cited as "Piraña" in Pitman et al. 2001), (0°39'25.685"S, 76°27'10.813"W; 216 m), and Tiputini Biodiversity Station (cited as "Tiputini" in Pitman et al. 2001) (0°37'55.397"S, 76°08'39.204"W; 216 m) Ecuador, between January 1994 and July 2002. These two sites are connected by continuous primary tropical rain forest at the margin of Yasuní National Park in the Ecuadorian part of the Amazon Basin located in Orellana Province. Both sites are at first sight very similar *terra firma* forest (non-floodplain) containing extremely diverse lowland forest vegetation and characteristic of the forests of the western Amazon Basin (Condit et al. 2002; Pitman et al. 2001; Erwin and Aschero [in preparation]). Precipitation is somewhat seasonal, 2.7 m of rainfall per year, with the dry and wet seasons running from approximately November to April, and May to October, respectively.

Samples

Sampling by insecticidal fogging was employed to gather the specimens we analyzed to determine species turnover of a component of species living in the canopy/understory fractal universes, a measure of at least $\frac{2}{3}$ of the biodiversity at this site (cf. Erwin 1982). In order to determine the insect biodiversity of the forested sites, we established two study plots (Lucky et al. 2002), one in 1994 (Piraña) and the other in 1997 (Tiputini). Each was a 100 m \times 1000 m area that consisted of ten 10 m \times 100 m transects spaced at 100 m from each other along the plot. Ten collection stations, each 3 m \times 3 m, were randomly located within each 10 m \times 100 m zone arrayed on both sides of a centerline. Fogging stations at each site were numbered 1–100 at the beginning of the study and were then, each one, used repeatedly for 9 sampling events across three years, "three seasons" per year (dry, wet, and wet to dry transitional). Canopy/understory sampling spanned eight years from January 1994 through July 2002 (intermittent funding as well as sporadic political unrest in Ecuador extended the field work at Tiputini), three at the Piraña site and parts of five years at the Tiputini site to account for trans-annual variation. In order to account for seasonal variation, sampling took place in January/February the dry season, June/July the wet season, as well as October, which represented a transition period between the wet and dry seasons. The fogging techniques have been described previously (Erwin 1983a, 1983b). The only modification made for this study as opposed to those previously undertaken was the use of 3 m \times 3 m sampling sheets suspended by

nylon string tied to trees or stakes and arranged one meter off the ground at each station (Fig. 1). Foggings were made from just above each sheet as a column (1 m to 'n' m high) into the canopy at 0345–0500 hours. Height of fog ascendancy was measured for all fogging events. Hence, the target was a column of forest including the understory above one meter and the canopy strata at each station. In this area, canopy strata vary from one to three levels, with some super-emergent trees rising above 40 m. None of the widely dispersed super-emergents was located over any of the fogging stations.

Specimens collected from each fogging event at Piraña were sorted and 14 target taxa were extracted, including the Coleoptera, for another purpose (monitoring Maxus Oil Company road building activities and their impact on forest arthropods). In order to test for β -Diversity, a plot at Tiputini was established in 1997. Subsequently, a portion of the beetles from both sites was resorted to acquire the 16 family-group taxa for the present project. We then sorted at least 600 samples, 300 or more from Piraña and 300 from Tiputini from like seasons, of many of the 16 family-group taxa to the level of morphospecies (Table 1). Two of these family-group taxa had been previously removed from all samples for other studies (Carabidae, *cf.* Lucky et al. 2002 and Cleridae for taxonomy). We focus here on two of the family-group taxa because only they reached nearly an asymptote on the species accumulation curve when samples from both plots were combined. No family-group taxon at this point in our investigation has reached an asymptote at one site. We discuss some other family-group taxa here to illustrate certain points.

In total, the area sampled within each of the two plots (Piraña and Tiputini) was 9250 m², a mere 1.11% of the entire plot area. Previous experiments have demonstrated that faunal re-population occurs within 10 days after fogging (Erwin unpublished data) and rapid re-population was again demonstrated with data from the present study at a time interval of four months. Thus, the sampling setup and methodology permitted re-sampling of the same stations at four-month seasonal intervals throughout the three-year study at Piraña without affecting species abundance and diversity (Lucky et al. 2002).

In order to provide a characterization of forest composition, trees within the two plots' ten transect zones with diameter at breast height (dbh measured at 1.33 m from tree base) greater than 10 cm were tagged by the senior author's team and subsequently identified by Nigel Pitman and colleagues (Pitman et al. 2001).

Analysis

We wanted to know if our sampling procedures of selecting 600 samples, one third of our total of 1800 samples, would be sufficient for comparisons between the two study sites. These compar-



FIGURE 1. Diagrammatic depiction of fogging event station with column of effective fog and tree architecture.

isons would have validity only if the Complementarity Index (see below) demonstrates that most of the targeted fauna at each site is included. In no family-group taxa sorted thus far did we achieve an absolute asymptote on the accumulation curves with 600 samples. We believe, however, that we are close enough using 600 samples to analyze the data from one family-group taxon (Curculionidae–Otidocephalini), and we were close enough using the 1200 samples of Carabidae for initial insights in the local distribution of beetle taxa in our area. Thus, these preliminary results are based on far fewer than our total 1800 available samples we took in the field over a period of 8 years. We recognize that each family-group taxon will respond differently to the Complementarity analysis depending upon its real diversity, i.e., the larger the taxon's diversity the greater is the overestimation bias (Colwell and Coddington 1994).

Analysis Tools

We used the EstimateS Version 6.01b program (Colwell 2000) to obtain the species accumulation curves and we used the Complementarity Index (CI) of Colwell and Coddington (1994) to determine the difference (or turnover) in faunas between the two sites. Sigma Plot 8.0 was used to graph the data from EstimateS. For explanations of the estimators we use here, such as ICE, ACE, Chao 1, Chao 2, and Jack 2, see Colwell and Coddington (1994) and documentation of the program EstimateS at <<http://viceroy.eeb.uconn.edu/estimates/>>.

RESULTS

Characterization of Forest Composition

Within the ten transect zones of the study plot at Piraña, 669 trees with dbh >10cm were found to represent 250 species and 51 families (data from Pitman, pers. commun.). Forty trees (5.98%) remain unidentified, so the true plot richness may be 9 to 15 species higher. The most common tree families, i.e., represented by more than 19 trees each, include (in order of abundance): Fabaceae (87 individuals), Arecaceae (60), Bombacaceae (57), Moraceae (46), Lecythidaceae (43), Burseraceae (36), Cecropiaceae (24) Myristacaceae (22), and Euphorbiaceae (19). The commonest tree is *Matisia malacocalyx* s. lat. (Bombacaceae) and is represented by 42 individuals.

The trees at Tiputini were similarly tagged by Erwin's team and subsequently identified, again by Pitman's team. Within the ten transect zones of the study plot at Tiputini, 623 trees with dbh >10 cm were found to represent 252 species, and 48 families (data from N. Pitman pers. comm.). Twenty-nine trees (4.65%) remain unidentified, so the true plot richness may be 5 to 10 species higher. The most common tree families, represented by 19 or more trees, include (in order of abundance) Fabaceae (82), Moraceae (57), Arecaceae (41), Bombacaceae (27), Cecropiaceae (34), and Myristacaceae (34), Lecythidaceae (30), Euphorbiaceae (27), Sapotaceae (27), Lauraceae (26), Meliaceae (20), and Burseraceae (19). The commonest species is the palm *Iriartea deltoidea* Ruiz & Pav. and it is represented by 40 individuals.

Although the most common tree species of western *terra firma* forests are represented in our plots, only part of the total regional tree species is represented. In addition to our plots, Pitman's team studied 22 other plots, each one square hectare, across the Yasuni region. He listed 1176 tree species (Pitman, pers. commun.). The two plots studied here have about 250 species each, thus each plot represents 21.42% (Tiputini) and 21.26% (Piraña) of regional tree species richness. However, because each plot has a different composition, together they represent about 34% of tree species richness in the Yasuni region.

As demonstrated above, tree composition at the two sites is very similar at the family level (CI

= 0.26), Fabaceae, Arecaceae, Moraceae, Bombacaceae, Moraceae, Lecythidaceae, Burseraceae, Cecropiaceae, Myristacaceae, and Ephorbiaceae are the commonest families at both sites. However, at the generic level, the difference is more pronounced ($CI = 0.52$) and at the species level, dramatically so ($CI = 0.73$) (Erwin and Aschero, in prep.).

Beetle Diversity

The canopy sampling regime from forest columns at Piraña, as described above, resulted in capture of some 1.7 million counted specimens belonging to 16 target taxa. The total sampling regime acquired, based on estimates of other taxa, indicate that we have 3.8 million specimens, 49% of which are ants. Beetles in the 900 Piraña samples accounted for 214,747 individuals, 13% of the total of fogging captures. This count was second in abundance at 22% to Diptera (although this dipteran abundance is because of one family whose populations burst out incredibly in the rainy season when fungus are available, i.e., Mycetophilidae). We detected no significant seasonal difference for abundance in the 16 target taxa (see below) across the nine seasonal fogging events at Piraña (ANOVA: $F = 0.39$, $P > 0.05$). From 300 of the samples at Piraña, plus another 300 like samples at the second site, Tiputini, specimens of 16 family-group beetle taxa were extracted for our study.

From these Piraña and Tiputini samples, a total of 15,126 adults representing 2010 morpho-species of the target taxa have been sorted to date (Table 1). For one family-group taxon, Curculionidae (Otidoccephalini), combining 300 samples from both sites proved adequate to nearly reach a species accumulation curve asymptote for the area (Fig. 2), whereas in Buprestidae (Fig. 3), Artematopodidae (Fig. 4), Cleridae (Fig. 5), and the rest of the families, at least 300 or more samples will need to be added to the database to reach a species accumulation curve asymptote. One other family, Carabidae, required analysis of 1200 fogging events to close in on an asymptote (Fig. 6). The Carabidae at Piraña were not adequately sampled with 900 samples, however the 300 samples of carabids that have been processed thus far from Tiputini provided enough additional species for a species accumulation curve to reach an asymptote for the local area. When these two family-group taxa were analyzed for Complementarity between the two sites, values were $CI = 0.29$ for otidoccephaline Curculionidae and $CI = 0.69$ for Carabidae (Table 1).

The Taxa

Artematopodidae ATRM (Fig. 7). The artematopodid beetles are known to be associated with mosses as larvae and adults are found on foliage. There are 60 described species worldwide, and they are relatively common in tropical forest canopies in the Amazon Basin. The study plots combined have 287 individuals representing seven morphospecies (Table 1) in the 600 samples studied. Occurrence was observed in 24.5% of those samples. The three most common species accounted for 94% of the abundance.

Buprestidae BUPR (Fig. 8). The "Jewel Beetles" visit flowers as adults and bore in plant tissue as larvae. There are 15,000 described species worldwide and these beetles are very common in the Amazon Basin. The study plots combined have 544 individuals representing 194 morpho-species (Table 1) in the 600 samples studied. Occurrence was observed in 47% of those samples. The three most common species accounted for 6.13% of the abundance.

Carabidae CARA (Fig. 9). The "Ground Beetles" (appropriately named in temperate region, however, in the tropics more than 50% of the species live on shrubs and trees) are for the most part predatory on other arthropods or their eggs, as both adults and larvae. Members of the dominant canopy genus, *Agra*, have been observed drinking plant exudates (Arndt et al. 2001). Two large

TABLE 1. Data for sixteen family-group beetle taxa. ACE, ICE and Chao 1 are estimators in the program EstimateS (see Methods); S Obs = Species observed; CI = Complementarity Index. Coleoptera Family-group codons are as follows: ARTM, Armatopodidae; ATTL, Attelabidae; BUPR, Buprestidae; CARA, Carabidae; CCAN, Ceratocanthidae; C-CRPC, Cryptocephalinae; CHYS, Chrysomelidae; C-HISP, Hispinae; CLER, Cleridae; C-OTID, Curculionidae, Otidoccephalini; C-ENTL, Curculionidae, Entiminae; CNTH, Cantheridae; ELAT, Elateridae; EROT, Erotylidae; MORD, Mordellidae; SCAR, Scarabaeidae; T-STRG, Tenebrionidae, Strongyliini.

Taxon	#		%									Feeding Guild	
	Samples	Occurrence	S Obs	Individuals	Singletons	Doubletons	ACE	ICE	Chao 1	CI			
ARTM	600	84	7	287	2	0	10	7.9	6.4			Herbivore	
ATTL	not yet processed											Herbivore	
BUPR	600	282	47	544	41	49	323	234	315			Herbivore	
CARA	1200	911	76	3536	37	58	475	477	473	0.7		Predator/ Nectivore	
CCAN	600	132	22	208	4	3	52	36	38			Fungivore	
C-CRPC	600	288	48	695	62	68	217	227	209			Herbivore	
C-HISP	1000	423	42	835	89	32	314	316	318			Herbivore	
C-ENTL	600	236	39	640	3	4	61	45	41			Herbivore	
C-OTID	600	291	49	572	4	2	43	37	39	0.3		Herbivore	
CLER	1200	600	50	1083	18	18	180	139	137			Predator	
CNTH	not yet processed											Herbivore/ Pollinator	
ELAT	600	447	75	1774	25	24	174	138	130			Herbivore/ Nectararies	
EROT	600	362	60	967	34	33	210	168	175			Fungivore	
MORD	1000	833	83	3000	45	54	428	361	347			—	
SCAR	1000	444	44	821	16	19	174	133	136			Herbivore/ Fungivore	
T-STRG	600	168	28	219	17	16	127	90	113			Fungivore	
Totals				15181	397	380							
					19.84%	18.99%							

FIGURE 2. Observed species accumulation curve and five estimation curves (ACE, ICE, CHAO 1, CHAO 2, JACK 2) for Curculionidae (Otidocephalini) with data combined from both sites.

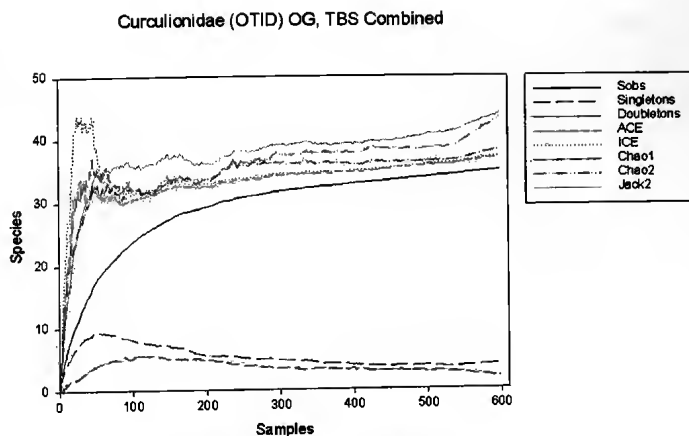


FIGURE 3. Observed species accumulation curve and five estimation curves (ACE, ICE, CHAO 1, CHAO 2, JACK 2) for Buprestidae with data combined from both sites.

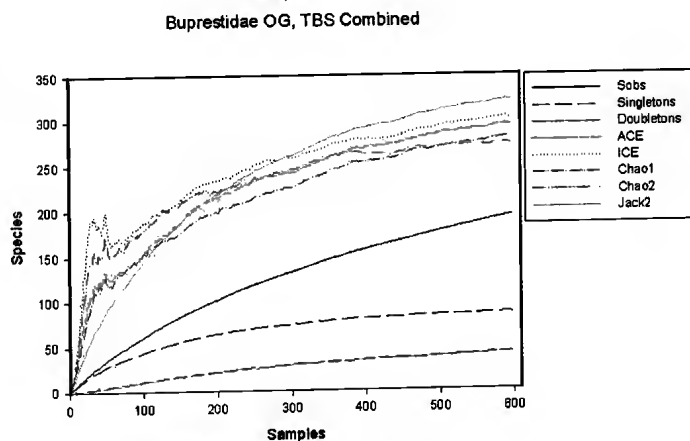
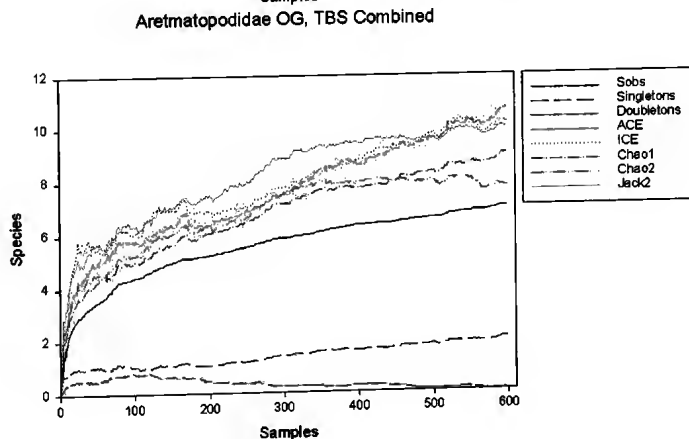


FIGURE 4. Observed species accumulation curve and five estimation curves (ACE, ICE, CHAO 1, CHAO 2, JACK 2) for Armatopodidae with data combined from both sites.



tribes have specialized as seed predators (Erwin 1981); however, these are not arboricolous species. There are 39,000 described species worldwide and these beetles are very common in the Amazon Basin. The study plots combined have 3536 individuals representing 462 morphospecies (Table 1) in the 1200 samples studied. Occurrence was observed in 76% of those samples. The three most common species accounted for 5.15% of the abundance.

Cleridae CLER (Fig. 10). The "Checkered Beetles" are mostly predators as adults and as lar-

FIGURE 5. Observed species accumulation curve and five estimation curves (ACE, ICE, CHAO 1, CHAO 2, JACK 2) for Cleridae with data combined from both sites.

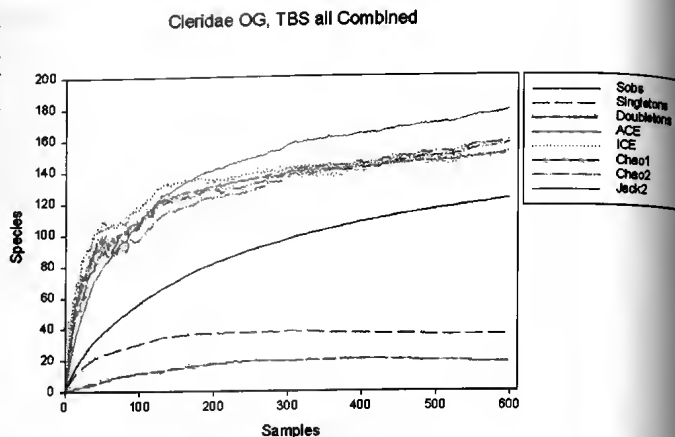
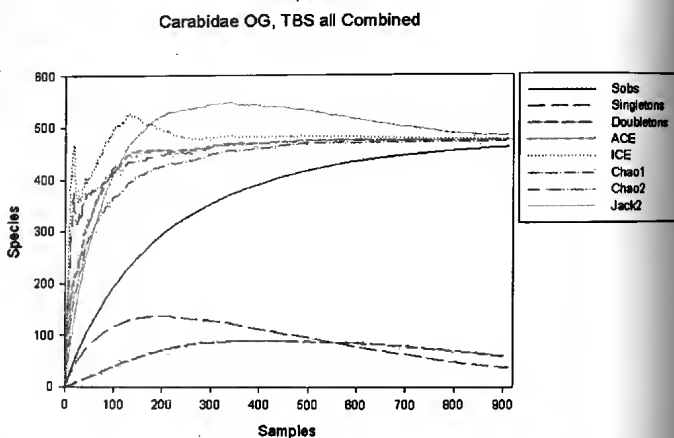


FIGURE 6. Observed species accumulation curve and five estimation curves (ACE, ICE, CHAO 1, CHAO 2, JACK 2) for Carabidae with data combined from both sites.



vae. There are 3400 described species worldwide; they are very common in the Amazon Basin. The study plots combined have 1083 individuals representing 122 morphospecies (Table 1) in the 1200 samples studied. Occurrence was observed in the 50% of those samples. The three most common species accounted for 35.94% of the abundance.

Curculionidae (Otidocephalini) OTID (Fig. 11). The otidocephaline beetles are known to be associated with several families of plants in which they mine stems. There are 35 described species in the New World; they are relatively common in tropical forest canopies in the Amazon Basin. The study plots combined have 572 individuals representing 35 morphospecies (Table 1) in the 600 samples studied. Occurrence was observed in 49% of those samples. The three most common species accounted for 44.9% of the abundance.

DISCUSSION

Patterns Observed

A consistent set of patterns emerged in the data for 14 of the 16 family-group taxa thus far investigated. In these taxa, even with the rigorous sampling regime, more samples than 600 are needed to know the universe of canopy/understory species in the local area (Figs. 3–5), and certainly more than 300 samples at one site, even for the smallest of families (Fig. 4). The only exceptions amongst the 16 family-group taxa were the otidocephaline *Curculionidae* (Fig. 2) that nearly



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FIGURE 7 (upper left). Image of one species of Artematopodidae (Genus *Artematopus*), length 5.0mm.

FIGURE 8 (upper right). Image of one species of Buprestidae (Genus *Leiopleura*), length 4.0mm.

FIGURE 9 (lower left). Image of one species of Carabidae (Genus *Otoglossa*), length 6.5mm.

FIGURE 10 (lower right). Image of one species of Cleridae (Genus *Axina*), length 7.0mm.

FIGURE 11. Image of one species of oditocephaline Curculionidae (Genus *Hammatostylus*), length 22.0mm.

reach an asymptote with 600 samples and the Carabidae (Fig. 6) that required 1200 samples, but only when samples were combined from both sites.

The difference in number of individual trees at Piraña (669) and Tiputini (623) is accounted for by a blow-down along two transects between the time of setting up the plot and its inventory by Pitman's team. Some 30 trees were felled in this blow-down and were not included on the identification list. Even so, both of our study sites represent accurately the expected tree composition of the *terra firma* forests in the equatorial Amazon Basin. The Piraña site accounts for 80.5% and Tiputini for 82.9% of the total 41 common species identified that dominate this type of vegetation in the Yasuni area (Pitman et al. 2001). For a more detail explanation of how similar western Amazonian forests are in terms of tree oligarchies, and particularly the Ecuadorian forests, see Pitman et al. (2001).

Analyses Compared

Even though we did not have all possible species at either of the two sites, we had indications that we had close to all the species of the "regional" fauna in two family-group taxa. So, we decided to do an analysis of complementarity for those. We predicted that we would get an overestimation of distinctness for the sites and this would be more exaggerated for the highly diverse Carabidae (cf. Colwell and Coddington 1994). Even so, based on the disparity between the CIs, the relationship between the two CIs was of interest, even if overestimated. This analysis hinted at a high degree of turnover for the carabids between the sites ($CI = 0.69$), and much less so for the oti-docephaline Curculionidae ($CI = 0.29$). This is the opposite of what we predicted. The former are predators and would not be expected to be dependent on the vegetation in some way as food. Lucky et al. (2002) showed that only palms significantly affected carabids negatively at Piraña, that is, the more palms the less carabid species richness. The weevils are herbivores and should reflect the marked degree of complementarity of tree species between the sites, but they do not. We do not know enough about the host plants for the weevils; perhaps they use only the commonest tree species as hosts which make up the majority of the tree flora at both sites (see above); therefore they could occur everywhere in this type of forest.

Even though members of both Carabidae and Cleridae are comparable predator taxa, the clerids (Fig. 5) were not sampled with the same efficiency as the carabids. The carabids form two distinct components of the fauna: ground dwellers and canopy dwellers. Almost no ground dwellers were sampled by fogging. Thus, the results are based on species that live in the canopy habitat. Whereas adult clerids concentrate on fallen trees and limbs in the understory, perhaps moving to the canopy occasionally where there is dead wood and their prey, there are many more chance captures with the fogging technique for clerids, and hence more singletons or doubletons turn up which affect the EstimateS algorithms.

A careful look at the larger dataset for Carabidae reveals that after inadequately reaching the accumulation curve asymptote at the Piraña site, more than 100 additional species were found at Tiputini in a mere $\frac{1}{3}$ of the available samples. Then, with both sites combined using various estimators, an asymptote was nearly reached. This was due to lowering the number of singletons and doubletons with additional samples. Are the other family patterns the same? Or, will the smaller families behave as did the Cleridae that were not adequately sampled at Piraña, nor fully sampled regionally even with 1200 samples. It is likely that some definitive conclusions might be reached when all 1800 samples of several families are analyzed. Until these are all processed, what does this preliminary step in the study tell us?

Results Applied

A faunistic and floristic inventory can be an important and necessary tool for planning and creating protected areas. Also, such inventories establish the basic information for monitoring community dynamics in space and time. Our study provides methodological information that could assist in the design and creation of protocols for entomofauna inventories in the Amazonian *terra firma* forests and elsewhere. We have demonstrated that it is likely possible to adequately sample insect family-group taxa for a local area in a relatively short time, inexpensively, even in an area of incredible diversity.

A series of fogging plots across a region at various floristically determined locals rigorously sampled, as were Piraña and Tiputini, may better describe the apparent mosaic distribution of canopy and understory arthropods (e.g., in plants, see Tuomisto et al. 2003). For all terrestrial arthropod species and other organisms, larger and more diversely sampled plots will be necessary (Erwin, in prep.) and undertaken on the scale accomplished by Tuomisto et al. (2003). This should lead to better understanding of species diversity and distributions, in turn leading to better strategic planning for conservation areas.

Equatorial forests are incredibly rich in beetle species dwelling in the canopy and understory vegetation, even at a local scale. The pattern of distribution of species is likely arrayed in a mosaic or discontinuous pattern rather than evenly distributed across the local landscape (Tuomisto et al. 2003). With our present knowledge, we cannot predict whether it is very subtle forest, soil, or climatic differences, or perhaps something historical that accounts for the pattern; likely, it is a combination of many things and probably a different suite of things for different taxa. Our results hint at a variable degree of species turnover across feeding guilds and across a forest mosaic within short distances even in similar forests in the western Amazon Basin, which in turn suggests that a conservation strategy of a few large conservation areas widely separated may not preserve a large share of existing biodiversity, namely insect species. Perhaps a new conservation paradigm may be necessary if we are to protect much of Earth's precious natural heritage in the fractal universe humans normally ignore, that of very small terrestrial arthropods.

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A Model for a Global Inventory of Ants: A Case Study in Madagascar

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For systematics to receive wide support across the biological and environmental sciences and attract public interest, taxonomic endeavors must be accelerated, products made more widely accessible across a broader community, and effort focused on global revisions of select taxa. Without this change in scope, systematics will never be in a position to respond to the needs of conservation or provide convincing examples of the role of taxonomy in society. Without this change, there will be little hope in attracting the broad and deep support needed to discover the vast amount of as-yet-undocumented diversity before it disappears.

Among the arthropods, ants (Hymenoptera: Formicidae) are an especially diverse and ecologically important group whose social behavior and ecological dominance have been the subject of intense biological study. These characteristics strengthen the selection of ants as a model taxon for global inventory. The model I describe is based on protocols tested in Madagascar to collect, inventory, process, prepare, and identify enormous numbers of ant specimens across diverse large-scale landscapes. In addition, the concurrent development of tools to accelerate species identification, description, and dissemination demonstrates the feasibility, challenges, and impacts of a global inventory of ants.

Systematists are charged with the intellectual enterprise of documenting and describing the history of life on Earth. They search for answers to the fundamental biological questions: What kinds of living things exist? Where do they live? How are they related? This is tedious and difficult work that requires enormous patience, experience and knowledge. Systematics has experienced a devastating erosion of its human capacity leading others to claim it is virtually dead (Godfray 2002; House of Lords 2002). The surge in funding and public awareness for conservation issues has almost completely overlooked taxonomy. Public and other funding bodies view systematics as unimportant and of little relation to the magnitude and urgency of the conservation crisis. They fail to appreciate the value of taxonomy.

But shouldn't society be clamoring for an increase in taxonomic information? Why are so few convinced that our goal should be to accelerate the collection and analysis of biodiversity information globally in response to the disappearance of natural habitats? Is it true that we don't need to know very much about what is living in a habitat to preserve it?

Biologists have argued that systematics provides an essential foundation for understanding, conserving, and using biodiversity (Blackmore 1996; Margules and Pressey 2000; Wilson 2000, 2003; Georgina et al. 2003). Yet systematists have been unable to convincingly demonstrate the vital role they could play in conservation. They have not demonstrated where taxonomy (or the lack of it) has had a profound impact on society. There are few examples that clearly illustrate the

practical applications of knowledge on species distributions to the saving of more species and to the improvement of human society (for examples, see Balmford 2003; <<http://www.bionet-intl.org/>>). Without clear examples, the public and the scientific community will not understand how knowing about more species will greatly help us preserve and conserve a greater number of them.

Systematists have few examples. This is in part, because they know so little about life on this planet — only a small fraction of life on Earth has been scientifically described and this fraction is distributed across many taxa (Blackmore 1996). Thus, systematists lack sufficient baseline global data on specific taxa that are accurate, comparable across sites, and fine-scaled to effectively demonstrate its role in conservation. They even lack a model of how to acquire these data in a time frame that is relevant to conservation. The existing near-catastrophic species extinction rate is often voiced as a call for action, a call to create a grass roots movement to establish the deep changes needed to tackle the vast diversity yet to be described. However, if nothing is done to change the glacial pace of current efforts and practice, it will take centuries to complete even a preliminary “Encyclopedia of life” on Earth (Wilson 2003). It is clear that if systematics is going to play a practical role concerning the preservation and development of natural systems, changes need to occur throughout the entire systematic process, from collecting to description, from publication to dissemination, and from public outreach to advocacy.

In this paper, I show how taxonomic data can be gathered, analyzed, and synthesized into useful products in a timeframe that meets the challenge presented by the rate of biodiversity loss. I test a model for accelerating the taxonomic process with the aims of providing the necessary data for effective taxonomy, and — most importantly — the tools for making data accessible and applicable to the conservation agenda. The model is tested on a key taxonomic group, ants, and in an especially threatened area, Madagascar. I describe the inventory procedure, processing facilities, data management, and identification tools developed and tested in Madagascar as part of the Madagascar Ant Diversity Initiative project (MANDI).

CASE STUDY: MADAGASCAR

Urgency

Madagascar has been identified as one of the world’s outstanding biological hotspots, harboring a unique and threatened biota, whose composition and origins are linked to the breakup of Gondwana (Battistini and Richard-Vindard 1972; Jolly et al. 1984; Storey et al. 1995; Lourenço 1996; Goodman and Patterson 1997; Goodman and Benstead 2003). As in many island environments (Gillespie and Roderick 2002), Madagascar’s indigenous terrestrial arthropods are in severe danger of extinction due to habitat deterioration and invasion of exotic species. Since humans colonized Madagascar circa 1500–2000 years ago (Burney 1987), it is estimated that as much as 80% of Madagascar’s original habitat has been destroyed (Sussman et al. 1996). Much of the island is now very species-poor secondary grassland, which is annually burnt and highly eroded.

Never has there been a more supportive political environment in which to address these threats in Madagascar. Over the next ten years, the Malagasy government plans to more than triple the number of protected areas and is committed to sustainable conservation planning. To accomplish these goals, areas of conservation importance must be determined. One major obstacle to the identification of areas for protection in Madagascar is incomplete knowledge of the island’s patterns of species richness, turnover, and endemism (Schatz 2002). It is unclear which of the remaining patches of natural vegetation should be of highest priority for conservation. What data exist are often at

inappropriate spatial scales required for conservation implementation, not standardized across sites, and focused on vertebrates, which represent only a small proportion of the biota.

Spatial Scale

Recent case studies confirm that shifting from broad-to-fine scale planning maximizes biodiversity conservation and that fine-scale data are usually required for implementation at local levels (Balmford 2003; Rouget 2003). In a case study focusing in on the Agulhas Plain within the Cape Floristic Region, fine-scale assessment was most important for heterogeneous and fragmented areas (Rouget 2003). Conservation assessment in the highly fragmented habitats of Madagascar will require fine-scale data to be gathered. For example, in eastern Madagascar, birds may be the least appropriate group to choose for fine-scale assessment whereas other taxa such as ants are far more sensitive instruments.

In a comparison of birds and ants at four reserves in eastern Madagascar (Parc National (PN) d'Andohahela, PN d'Andringitra, PN de Masoala, Réserve Spéciale (RS) d'Anjanaharibe-Sud), birds showed very low levels of complementarity (distinctness) and turnover between elevations within localities and between all four localities (Fisher 1997). Consequently, prioritization of protected areas based on preserving representative species of bird may not equally protect taxa with higher levels of turnover, such as ants, amphibians, reptiles, or insectivores. For example, based on the four localities, the RS d'Anjanaharibe-Sud had the highest species richness of birds and therefore could be chosen to receive the highest priority for protection. The RS d'Anjanaharibe-Sud also had the highest species richness for ants. Although 96% of the tropical forest dwelling bird species from the four localities would be preserved in the RS d'Anjanaharibe-Sud, only 47% of the ant species from all four localities would be protected. If high levels of turnover drive conservation evaluation, then data on ants and possibly other invertebrates (Olson 1994) are critical. MANDI is a model solution for this need and can provide vital fine-scale data for conservation planning and monitoring efforts.

Ants

Ants are of signal ecological importance. Our understanding of their taxonomy, diversity patterns, evolution and ecology, however, is limited and does not reflect either their crucial role in global ecosystems or their potential importance in land management and conservation (Agosti, et al. 2000). It is estimated that only half of the world's ant species — currently numbering about 11,000 — have been described. A more complete inventory of the world's ant fauna is essential to advance understanding of ant ecology, evolution and behavior, and to take full advantage of their demonstrated value in conservation priority setting, biomonitoring, and biological control. To inventory, describe, and classify all ant species are goals that should be embraced by the entire systematic and conservation community.

Until recently, the ant fauna of Madagascar was poorly known. It, thus, provides an ideal testing ground for developing a global ant inventory procedure (Fisher 2003). The objectives in Madagascar were to complete an overview of the ant fauna for taxonomic and evolutionary studies, and to create a map of diversity patterns for use in land management and conservation priority setting. Thus, the inventory goals were not to simply create a list of species for each locality, but to produce the necessary specimens for detailed systematic analysis plus the biodiversity data for the many users across the conservation community.

INVENTORY MODEL OVERVIEW, METHODS, TOOLS, AND IMPACTS

Inventory

Solutions to collecting and processing specimens were addressed by developing efficient, scalable workflows, termed the "industrial strength" approach by E.O Wilson. The success required new specimen capture methods, fine-scale specimen processing techniques, establishment of industrial-sized processing centers, integrated data management, and intensive taxonomic training.

The overall collecting and inventory design is based on the hierarchical labor cost of taxonomy (Table 1). The least expensive aspect of systematics is the collecting. The next stage, data and specimen processing, ranks second, whereas taxonomic identification and description is the most expensive part of the process. Collecting and processing schemes, therefore, must maximize taxonomic product and reduce its costs. For processing, this translates to providing taxonomists the minimum number of correctly prepared and databased specimens of the greatest number of species. For collecting, this means choosing field sites that maximize new species capture and choosing methods that maximize species collection per endeavor.

TABLE 1. Relative skill level, time, and costs of personnel involved in collecting, processing, and identifying ant specimens in Madagascar.

<i>Skill and Pay Level</i>	<i>Activity Description</i>	<i>No.</i>
Field Team: 6 months/year		
Assistant level I	local field assistance	3
Assistant level II	field collection	4
Field leader, level IV	permits, field preparations	1
Processing Lab: all year		
Assistant level I	sort all specimens to order; label	3
Assistant level II	sort ants to genera	2
Assistant level III	mount representative ant species	4
Lab Manager, level IV	train and manage	1
Identification: all year		
Assistant level II	specimen data entry	1
Assistant level IV	sort to species	2

means choosing field sites that maximize new species capture and choosing methods that maximize species collection per endeavor.

Site selection methods. The strategy was to maximize collection efficiency and species-coverage by sampling the full range of habitats found in Madagascar, based on vegetation, climate, elevation, and geological substrate. Previous fieldwork on the island has shown that these four factors strongly influence the species composition of ants on the island (Fisher 1996, 1998, 1999b). Based on the principle of sampling representative habitats and regions, 100 localities were identified for field collecting (Fig. 1). Due to the complex topography and high rainfall, the expeditions were some of the most complex and logistically challenging that have ever been conducted in Madagascar. Results from MANDI demonstrate that site selection based on unique combinations of bioclimate and substrate is an efficient method to capture representative ant species from regions where there are limited pre-existing collections (unpublished data).

Collecting methods. Ant researchers have been leaders in the development of efficient collecting and processing techniques (Fisher 1999a, 2002; Agosti et al. 2000; Fisher and Robertson 2002; Longino et al. 2002). These studies have evaluated: (1) efficiencies of different methods to capture ant assemblages; (2) effect of habitat on method efficiencies; (3) effects of (sub)sample size and spacing on completeness and ranking of species richness; (4) completeness of beta-diversity and complementarity values; and (5) use of surrogate or indicator taxa for estimating total ant richness. MANDI employs a complement of inventory techniques that have been proven to maximize

capture-rate of species per effort. These comprise the following principal quantitative methods: litter sifting, beating low vegetation, and pitfall traps. These techniques involve taking 25 (beating) or 50 (pitfall, leaf litter) subsample collections along a 250m transect for each method. The use of quantitative methods provides, in addition to a species list for each site, information for measuring completeness of the inventory as well as turnover or complementarity of species assemblages between sites (Fisher 1999a). In addition to the quantitative transects, light traps, Malaise, and manual hand collecting are employed. During a three year period, 2000–2003, 54 sites were inventoried across Madagascar using 3280 leaf litter samples, 1350 beating samples, 2700 pitfall trap samples, 216 nights of light trapping, 1350 days of Malaise trapping, and 5900 hand collections. Surveys confirm that the most efficient combination of collecting methods for ants in forest, spiny thicket, and grasslands is leaf-litter sifting plus hand collecting (Longino and Colwell 1997; Fisher 1999a; Fisher and Robertson 2002; Longino et al. 2002).

Processing

The challenge of processing specimens is its sheer magnitude. With little effort, one can collect millions of arthropod specimens. How do you extract relevant specimens for taxon-specific goals but at the same time make accessible the balance of the remaining millions of specimens for the global taxonomic community? To accomplish this, we developed a specimen-processing protocol that relies on extensive training of personnel, highly partitioned division of labor, and a built-in checking system to insure accurate data capture (Table 1).

Specimen processing is more costly than collecting because it requires more people and an enormous investment in taxonomic training (Table 1). The cost in training greatly increases as taxonomic rank decreases. It should be noted, however, that the cost to train technicians to sort insects to order is very low and should be encouraged in all arthropod inventories. Sorting to order greatly increases the accessibility of specimens to taxonomists.

From 2000–2003, we estimate that more than 2 million arthropod specimens were processed and sorted to taxonomically accessible groups, and over 300,000 ants were pinned and labeled. Specimens were sorted at the processing facility in Madagascar and then sent to the California



FIGURE 1. Madagascar: location of the 100 localities that were identified for field collecting

Academy of Sciences for distribution to over 75 collaborating taxonomists. This approach emphasizes speedy shipping of specimens to active taxonomists.

Ant specimens are removed from each collection sample and sorted to genus. To save preparation costs and reduce taxonomists' specimen-handling time, only a subset of material is prepared. For ants, this translates to mounting one representative of each morphospecies from each mass sample or subsample (pitfall, Malaise, litter, beating, light) and nine representatives from each manual hand collection. Because trained preparators make the decisions about what representative specimens to mount (as opposed to the thousands that might stay in the vial), only a subset is prepared. This saves money in preparation and taxonomists' time in identification. It also reduces the costs of storing and managing prepared specimens of common species that would have been mounted by a mass preparation facility.

Even though this approach results in preparation of a small proportion of all collected specimens, it still represents an excessive number of common species, and at times too few rare species. For example, if a species is found in 1000 samples, this common species will be mounted at least 1000 times. Species found only in a few collections, however, may not be always sufficiently prepared and additional specimens may need to be retrieved from the alcohol samples during taxonomic revision. This is a simple problem, which is easily and cheaply resolved. The problem of mounting of too many common species, however, is costly to correct. Correction would require the preparators to have sufficient taxonomic knowledge to identify the common species that should not be mounted. This could be done if the collections are from a localized region, such as one national park, where the set of common species is constant. It is much more difficult to achieve if the samples are from a wide geographic region. The cost of training preparators may outweigh the savings in managing the excessive common specimens. I know of no simple solution to this problem of occasionally burdening the taxonomist with the handling of large numbers of the most common species.

Data management is an important aspect of the processing facility. Data acquisition is integrated with the demands of specimen processing, fundamental to label production and specimen management. We use the program Biota (Colwell 1996) for specimen data management. We have a centralized control of locality and collection data entry and regional input of specimen level data. Each pin and vial is labeled with a unique object code. Though all vials and pinned material carry unique codes, we currently database only specimens from unique collection records for each species. These are the minimum data necessary to fulfill the needs of taxonomists and to map biodiversity. More in-depth studies that compare rates of species accumulation will require additional data entry (every specimen) and will require an order of magnitude more effort in data entry.

Tools for Accelerating Taxonomy

MANDI has successfully demonstrated the feasibility of collecting and processing specimens at a global scale. New methods were invented and tested for collecting ants and industrial-sized processing centers were established. The enormous amount of material collected and processed, however, presents daunting new challenges: (1) how best to accelerate the analysis and synthesis of biodiversity data, and (2) how can the project achieve its goals to revise all ant species in Madagascar, including the description of 800 new species, and then disseminate this information in a time frame that contributes to conservation decisions?

Nothing can replace the countless hours of careful observation necessary to understand variation and to delimit species boundaries. New technologies, however, are being developed to overcome the most significant bottlenecks in the process of describing and identifying specimens. The

necessary steps are: (1) enable more people to participate collectively in the taxonomic process; (2) drastically reduce the number of steps in the documentation, collation, publication, and dissemination of the products; and (3) permit a broader audience to experience and use taxonomic products, thus increasing the value of systematic research.

As part of MANDI, the tools being developed include: (1) access to integrated backbone taxonomic information; (2) digital imaging technology for identification and description; and (3) online infrastructure for digital collation and publication of taxonomic products (species descriptions, maps, etc.). These tools simultaneously address two of the most important issues facing the practice of taxonomy: a need to reduce the number of steps required to identify and describe taxa in order to save time, and an equal need to improve access to and visibility of taxonomic products.

Building the integrated foundation: the three pillars. Unlike other disciplines where publications are rarely accessed after five years, taxonomists need continued access to the entire 250 years of historical literature stored in specialists' museums and libraries. Every step forward, every new piece of data, must be first filtered through this mass of historical information. This enormous burden could be immediately mitigated through online integration of the three pillars of taxonomic knowledge: (1) catalog information; (2) primary taxonomic literature; and (3) images of primary types.

The portal AntWeb <<http://www.antweb.org>> was created to provide access to images of all primary type material in Madagascar, with links to existing catalog information (e.g., <antbase.org>) and digital versions of the original and subsequent relevant redescrptions (William L. Brown, Jr. Memorial Digital Library) (Agosti and Johnson 2002; Dalton 2003). For example, AntWeb includes images of all primary types of the 71 endemic *Strumigenys* in Madagascar, including links to catalog information and original descriptions from Fisher (2000). With little additional effort and cost, the entire taxonomic backbone of the 418 named ant taxa in Madagascar can be made available to everyone through AntWeb.

An image is worth 1000 words. Because the state of ant taxonomy leaves most regions of the world without accurate identification keys to species, the process of identifying specimens is a huge task, costing much more than the collecting and processing of specimens. One of the most significant bottlenecks in the process of identifying specimens is the necessity to examine relevant type material, a procedure both time consuming and costly — but absolutely essential where faunas are incompletely documented and without identification keys. MANDI has collected an estimated 1000 species of ants in Madagascar, representing 300,000 pinned specimens, all of which require identification. Unfortunately, the literature cannot be relied upon for identification because species descriptions in general do not always have accurately detailed descriptions of species limits, much less illustrations. The current procedure for identification relies on visiting type collections or borrowing type specimens, both of which include the difficult step of identifying the location of types. This problem, as illustrated with the ants from Madagascar, is shared by all poorly known taxa and is thus a problem for all inventories and identification efforts (Stevenson et al. 2003).

Because many of the historical ant species descriptions are less than 100 words, an image will go a long way in conveying information on the specimen in question. Digital imaging technology is being used in MANDI to overcome the bottleneck of specimen identification by providing images of named taxa (types) and unnamed (new species). These high resolution images are an in-focus composite of ten to forty images created using the Syncroscopy Automontage software (Fig. 2). A standard suite of images is taken of each specimen: head in full-face view, profile, dorsal and an image of the label.

In Madagascar, where we are documenting a fauna from scratch, images are used to record

species as they are discovered and defined, providing placeholders for information and a quick reference for identification. The images represent named and unnamed species and grow as fast as species are discovered. The images are not a key, but with the AntWeb comparison tools, they facilitate comparisons of characters and species. Without AntWeb, comparisons would require access to collections of all possible species, a time consuming process that also presents risks to the specimens.

With AntWeb, a researcher will begin by reviewing all species of the genus on AntWeb, comparing images of similar taxa. If a working key has been already established, this key is used in conjunction with AntWeb to confirm identification

and present users a reference to characters mentioned in the key. This tool is powerful because it includes all known named and unnamed taxa and includes geographic and colony variation. Images and AntWeb do not replace the enormous time needed to study and define species limits; they are tools to facilitate documentation and identification of specimens.

Digital imaging technology, combined with the ease and speed of distributing data through the Internet and other media, promise immense change to this whole identification and documentation process. Type specimens and entire regional faunas can now be imaged in great detail and made instantly available to the scientific community worldwide. Entire collections of types can be published digitally within weeks for a fraction of the cost of publishing typical printed catalogs. Such an effort has resulted in a large positive change in the rate at which we can document the ant fauna of Madagascar.

Publication. Technology is used to both acquire data and then manage and assemble data elements for publication and revision. The aim is to use the information gathered during the inventory (collection and locality data) and identification process (images, notes on diagnosis) as integral pieces of any published revision. The revision becomes the collation of data acquired during the collecting, processing, and identification steps. Specimen databases are used to create distribution maps and the image library developed to identify specimens provides the necessary illustrations for species descriptions. The challenge is to develop a protocol for online publishing of revisions with the least number of steps that satisfies the requirement of the zoological code and facilitates the integration of results into existing online taxonomic databases (type, descriptions, and catalog).

Public access. Historically, systematists have concentrated on naming and describing species, with little attention given to the final product and how those outside taxonomy could use it. Most biodiversity information languishes in inaccessible journal articles, books and museum collections. As much as ninety percent of all described species have never been incorporated into identification manuals, or regional floral or faunal summaries, and, thus, the majority of taxonomic products have remained in low-circulation journals hidden in specialists' libraries. Rarely has taxonomic research resulted in accessible and widely useful products. User-unfriendliness of resources is the principal reason why there is not a broad base of public support clamoring for an increase in taxonomy.

BROADER IMPACTS

Renner and Ricklefs (1994) claim that systematists should not see themselves as "service providers", for this will take away from the intellectual validity of the discipline and sap it of it



FIGURE 2. Image created using Syncroscopy Automontage software.

vitality. I disagree and feel that in addition to the academic enterprise of hypothesis driven systematics, the systematics community needs to develop products that have a wider and more practical use across the applied and basic sciences, especially for the protection and management of biological resources. Renner and Ricklefs (1994) are concerned that it is detrimental to the profession for systematists to devote too much time conducting inventories because it requires precious taxonomic expertise to identify the specimens. On the other hand, if systematists facilitate the creation of tools permitting nonspecialists to identify specimens, parataxonomists can ease the burden of identification. Systematists must view species description as more than just putting names in lists. They must view their work as the access point for all users of that piece of the biodiversity puzzle and see their job as making his/her work accessible.

REPRESENTATION

Inventory provides baseline documentation of natural occurrence of wild species, and is a crucial first step in mapping conservation priorities. This map is required by all who share the aim of preserving the greatest representation of biodiversity in Madagascar. However, the usual taxonomic products — monographs and species lists — are not sufficient to ensure that biodiversity data are incorporated in local and national conservation decision-making processes. Biodiversity planners and decision makers in governments, agencies, and non-governmental agencies (NGOs) are unaware that these data exist and are not accustomed to including data on terrestrial invertebrates. To ensure that our data are used for conservation planning in Madagascar, we tailor our results toward practicality. This required development of strong relations with local conservation and government agencies so we would understand their policy approaches and decision-making needs. Most importantly, this has required understanding the spatial scale of the conservation issue, and the generation of maps and analyses at the appropriate scale. In collaboration with the Jet Propulsion Laboratory in the U.S., we are generating species richness maps of Madagascar based on predicted species distribution, remotely sensed environmental layers and a novel model algorithm allowing to make use of the standard sampling techniques for ants (Fig. 3).

Our ultimate goal is to develop a Biodiversity Center staffed by well-trained Malagasy scientists that will provide short- and long-term benefits to biodiversity and conservation efforts. The Center will promote understanding of the use of biodiversity data in planning land management and conservation systems, and provide baseline biodiversity data for sound conservation and sustainable use planning. The Center will dramatically improve ability to respond to local conservation issues, and to ensure that biodiversity results are disseminated to a broad audience of users. The training of Malagasy nationals and scientists to participate in conservation decision making in their country is an extremely effective way to ensure long-term commitment to conservation on this unique island.

CONCLUSION

The increasing loss of biodiversity presents a daunting challenge to taxonomists and requires the discovery and analysis of biodiversity at a greatly accelerated pace. If we are really serious about “zero biodiversity loss” in Madagascar and elsewhere, then conservation planning needs to be based more fundamentally on biodiversity data, and this requires taxonomic knowledge. The renovation of systematics, as proposed here, is an extremely ambitious program requiring innovation, and large-scale application of tools in systematic research, from collecting to dissemination of results. In addition, this initiative requires the systematic community to work together at a level never before realized, focusing attention on global revision of select taxa and ensuring the repre-

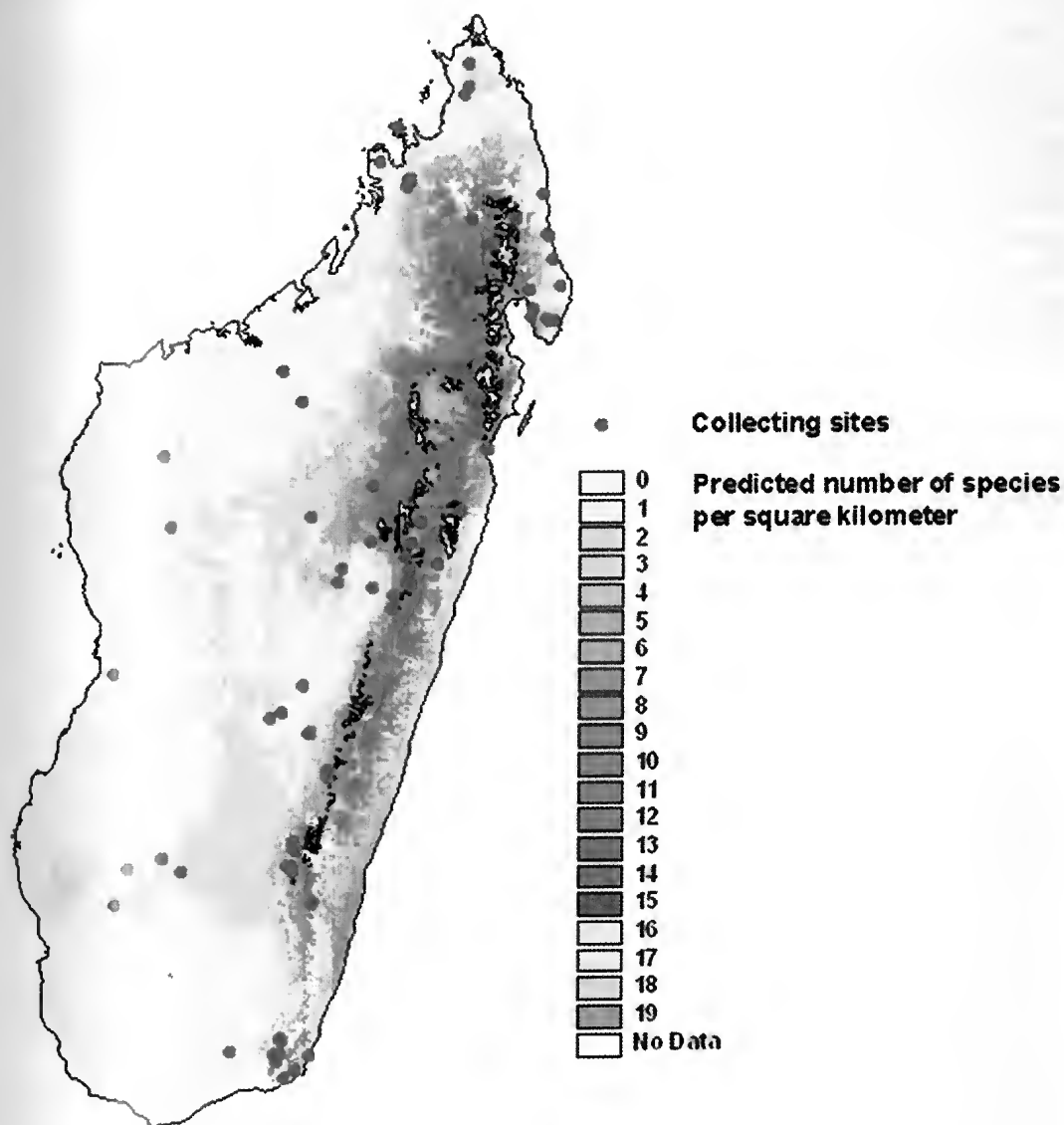


FIGURE 3. Sample species richness map of Madagascar based on predicted species distribution.

sentation of results in the conservation process, thereby enhancing the perceived value of taxonomy.

MANDI has demonstrated the feasibility of rapid collection and processing of ant specimens. This model, combined with innovations in imaging technology, has set the stage for accelerated discovery and documentation of global ant species diversity. The model proposed here can be applied across disciplines and toward other inventory efforts. Little time remains for the documentation of global biodiversity. Taxonomists, equipped with modern tools, have a chance to move systematics to the forefront of conservation and attention of the public. With increased taxonomic output and improved public access and visibility, public support for the discovery of life on this planet should follow.

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Conserving Biodiversity in Vietnam: Applying Biogeography to Conservation Research

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Vietnam has recently become the focus of renewed research efforts, whose results have highlighted the country's endemic biota and intrinsic species richness. The roots of this diversity are multiple and include Southeast Asia's complex geological and climatic past, Vietnam's wide range of latitudes (23° to 8°30'N) spanning a subtropical-tropical transition zone, and the country's relatively hilly and mountainous topography. The region has attracted the interest of biogeographers since the mid-nineteenth century and a variety of biogeographic units and hypothesized distribution patterns has been derived from studies of Southeast Asia's diversity. Multi-taxon surveys were undertaken in three little-studied and currently unprotected areas to aid in conservation efforts by adding to species diversity and distribution records and by examining the underlying patterns of biodiversity distribution. Results include new taxa, generic revisions, new country records, and significant range extensions. Data are consistent with some but not all of the proposed biogeographic patterns; both geographic scale and taxonomic group appeared to influence the results.

Situated along the eastern margin of the Indochinese Peninsula, Vietnam covers roughly 329,500 km² and is bordered to the north by China, to the west by Lao People's Democratic Republic (Laos) and Cambodia, and to the east by the South China Sea (known in Vietnam as the East Sea). Vietnam lies at a crossroad of biological diversity. A north-south orientation of more than 1650 km incorporates biotic regimes from the temperate Himalayas and the Chinese Palearctic zone in the northwest and northeast, the northern Indian zone to the west, and the tropical Malaysian zone to the south.

In the early to mid-1990s, Vietnam achieved global recognition for its unique and endemic species, generated in particular by a rush of large mammal species "discoveries" and rediscoveries emanating from the Truong Son Mountain Range (also known as the Annamite Range or Annamite Cordillera). These findings encompass six mammal species,¹ including the 85–100-kilogram saola (*Pseudoryx nghetinhensis*), an entirely new genus in the oxen family and the largest land-dwelling mammal described since 1937 (Amato et al. 1999; Pham Mong Giao et al. 1998; Pine 1994; Schaller and Vrba 1996; Surridge et al. 1999; Vu Van Dung et al. 1993). In addition to larger mammals, an impressive array of other organisms have recently been uncovered in this and other areas of Vietnam between 1992 and 2004, including over 200 taxa of vascular plants (Regalado in litt.

¹ Large-antlered muntjac (*Muntiacus vuquangensis*), Annamite muntjac (*Muntiacus truongsonensis*), Roosevelt's muntjac (*Muntiacus rooseveltorum*), saola (*Pseudoryx nghetinhensis*), Heude's pig (*Sus bucculentus*), and Annamite striped rabbit (*Nesolagus timminsi*).

2003), three birds,² three turtles, four snakes, 14 lizards, 31 frogs, and, since 2000 alone, 29 fish and over 500 invertebrates (Bain et al. 2003; Eames et al. 1999a; Eames et al. 1999b; Eames and Eames 2001; Zoological Record 2002).

These discoveries are coming to light now for several reasons. First, there has been a general increase in scientific research as Vietnam emerges from decades of political strife. Second, scientists — both Vietnamese and foreign — have increasingly, if sporadically, been given greater access to sensitive military buffer zones along the border with contiguous countries, where much of Vietnam's remaining naturally forested areas lie.

A third and related factor contributing to the large number of new species is the country's intrinsically high rate of species richness and endemism. Using data from the World Atlas of Biodiversity (Groombridge and Jenkins 2002) on plant, bird and mammal species richness per unit area, Vietnam ranks 25th in the world in terms of species richness. Examples of this diversity can be found across taxonomic groups. Vietnam's vascular plants have remarkable levels of species richness and endemism for such a small country, particularly in light of the taxonomic work that still needs to be done. Botanists estimate there to be around 13,000 species of vascular plants in Vietnam, 8,000 of which have been identified to date. This represents a little over 2% of the world's currently described species (Lecointre and Le Guyader 2001; Rundel 2000). Within the family Cycadaceae, Vietnam harbors 24 species of cycad, representing over 12% of the world's cycad species and subspecies (Donaldson 2003; Nguyen Tien Hiep and Phan Ke Loc 1999). Another example of elevated species richness can be found in the primate community. Twenty-seven primate taxa (19 species and eight subspecies) in the families Loridae, Cercopithecidae, and Hylobatidae live in Vietnam, seven of which are endemic to the country (Brandon-Jones et al. 2004).

Patterns of endemism in Vietnam are not well researched, but to date elevated floral endemism has been recorded in the northwest's Hoang Lien Son Range, the limestone regions of Cao Bang Province, Pu Mat and Pu Luong Nature Reserves in the northern Truong Son range, the Da Lat Plateau and adjacent montane areas of the southern Truong Son range, and the forested dunes and semi-arid slopes along the south-central coast near Nha Trang, Cam Ranh and Phan Ranh (Rundel 2000; Fig. 1). In some parts of Vietnam, such as the Fan Xi Pan massif in the northwest, the rates of vascular plant endemism rise to 40% (Nguyen Nghia Thin and Harder 1996). Faunal endemism in Vietnam is the highest in Indochina (Vietnam, Laos, Cambodia) (MacKinnon 1997). This may be due in part to a sampling artifact: Vietnam is currently better known than the other countries.

HISTORICAL AND CURRENT CONDITIONS

Vietnam's wealth of biological diversity stems from its complex geology and climate and its geographic location. The dynamic nature of these conditions both now and in the past has strongly influenced the biological richness of the country. Geologically, Southeast Asia is one of the world's most complex regions, at the interface of three converging continental plates: Eurasia, Indo-Australia and the Philippine Sea plates (Hall 1998). Vietnam itself comprises a collage of continental fragments that broke off sequentially from the "supercontinent" Gondwanaland 400–200 million years ago and migrated north to fuse at higher latitudes (Metcalf 2001). Due to this complex geological history, Vietnam's mountains are composites of marine sediments, rocks of metamorphic and volcanic origin, and ancient uplifted basement formations (Fontaine and Workman 1978; Hutchinson 1989).

² Black-crowned barwing (*Actinodura sondangorum*), golden-winged laughingthrush (*Garrulax ngoclinhensis*), and chestnut-eared laughingthrush (*Garrulax konkakinhensis*).

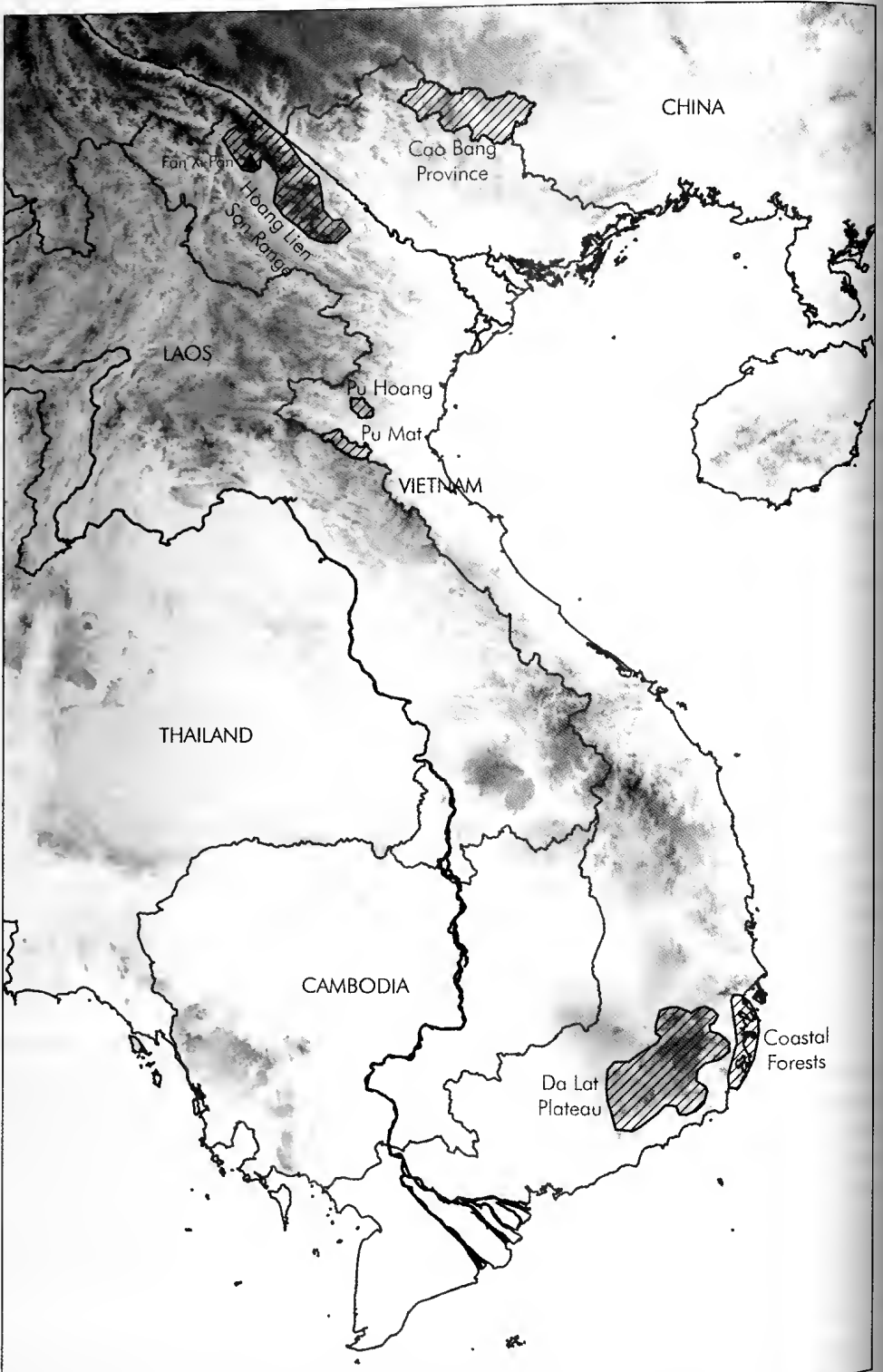


FIGURE 1. Areas of Vietnam (shaded) with high recorded floral endemism. All boundaries are approximations.

A more recent geologic event, the India-Eurasia collision about 50 million years ago, had profound impacts on Southeast Asia's evolutionary history, introducing new groups of organisms, creating dispersal barriers and modifying the climate (Hall 1998; Morley 2000). The rising of the Himalayas over the last 20 million years effectively cut off the exchange of species between the Palearctic and Indo-Malayan realms. This barrier, reinforced by increased climatic cooling after the Miocene, isolated Indo-Malaya and created conditions for species divergence (Jablonski 1993; Macey, et al. 1998). Additionally, the rise of the Tibetan Plateau as a result of this impact shifted rainfall, winds and other climatic patterns in East and Southeast Asia to become more monsoonal and strongly seasonal, increasing habitat diversity (An 2000; Clift et al. 2002).

Long-term oscillations in climatic conditions seem to have greatly affected distribution and dispersal of species in Southeast Asia. Starting in the Tertiary, global cooling events led to falling sea levels and an increase in the amount of exposed land area (Bennett 1997; Hewitt 2000). Unlike large land masses, such as South America, where sea levels 70 or 100 m below present levels had little effect, the smaller land areas and island archipelagos of Southeast Asia lie on the shallow Sunda Continental Shelf and their connectivity is strongly affected by sea level fluctuations (Heaney 1991). At 75 m below present level, the submerged shelf formed a bridge that likely served as a corridor between mainland Southeast Asia and the Sunda Islands, including Sumatra, Java, and Borneo (Voris 2000; Fig. 2).

Increased land area, coupled with a reduced South China Sea, led to decreasing moisture content of monsoon winds, resulting in cooler, drier conditions (An 2000; Zhou et al. 1996). Montane forest vegetation descended to lower levels, supplanting lowland evergreen rainforest forms, and grassland biomes replaced rainforests in more seasonal areas. During interglacial periods, the climate became warmer, wetter and less seasonal, and evergreen rainforest habitats expanded to retake higher elevations and latitudes; sea levels also rose to cover continental shelves, cutting off the land bridges (Kershaw et al. 2001; Morley 2000). These changes allowed populations in Southeast Asia to go through cycles of divergence and re-colonization, contributing to the high levels of species richness and endemism that now characterize the realm (MacKinnon 1997).

Contemporary seasonal climate fluctuations also shape Vietnam's biodiversity. Seasonality increases as one moves from south to north, away from Southeast Asia's perhumid core centered on Borneo, Sumatra, and the tip of Peninsular Malaysia. The dominant climatic feature is the monsoon circulation pattern, which directly influences the seasonality of rainfall. In the winter, strong north-east monsoon winds are produced as air flows from cold high pressure areas in Asia along the eastern edge of the Tibetan Plateau towards a hot low pressure zone over Australia, bringing dry winds to some of Vietnam. In the summer, southwestern monsoon winds flow from high-pressure areas over Australia and the Indian Ocean towards the interior of China, releasing water picked up over the seas as summer rains (An 2000).

These dynamic circulation patterns interact with regional land and ocean configurations, exposing Vietnam to a wide variety of rainfall regimes. Vietnam's hilly and mountainous topography influences the distribution of species and biotic communities by mediating temperature and humidity both locally at different altitudes and at a landscape level via rain shadow effects. Vietnam's elongated shape covers 14 degrees of latitude north to south, encompassing a wide range of climates and topographic relief overlying a variety of rocks and soils. The combination of local microclimates and the soil and substrate complexity has, in turn, shaped vegetative communities (Rundel 2000). Vietnam's major topographic feature, the Truong Son Range, runs roughly north to south along the Vietnam-Laos border and into south-central Vietnam. It forms an important barrier between the moist uplands of Vietnam and the drier monsoon forests of Laos and Cambodia and traverses the transition zone between the subtropical northern and the tropical southern climates.

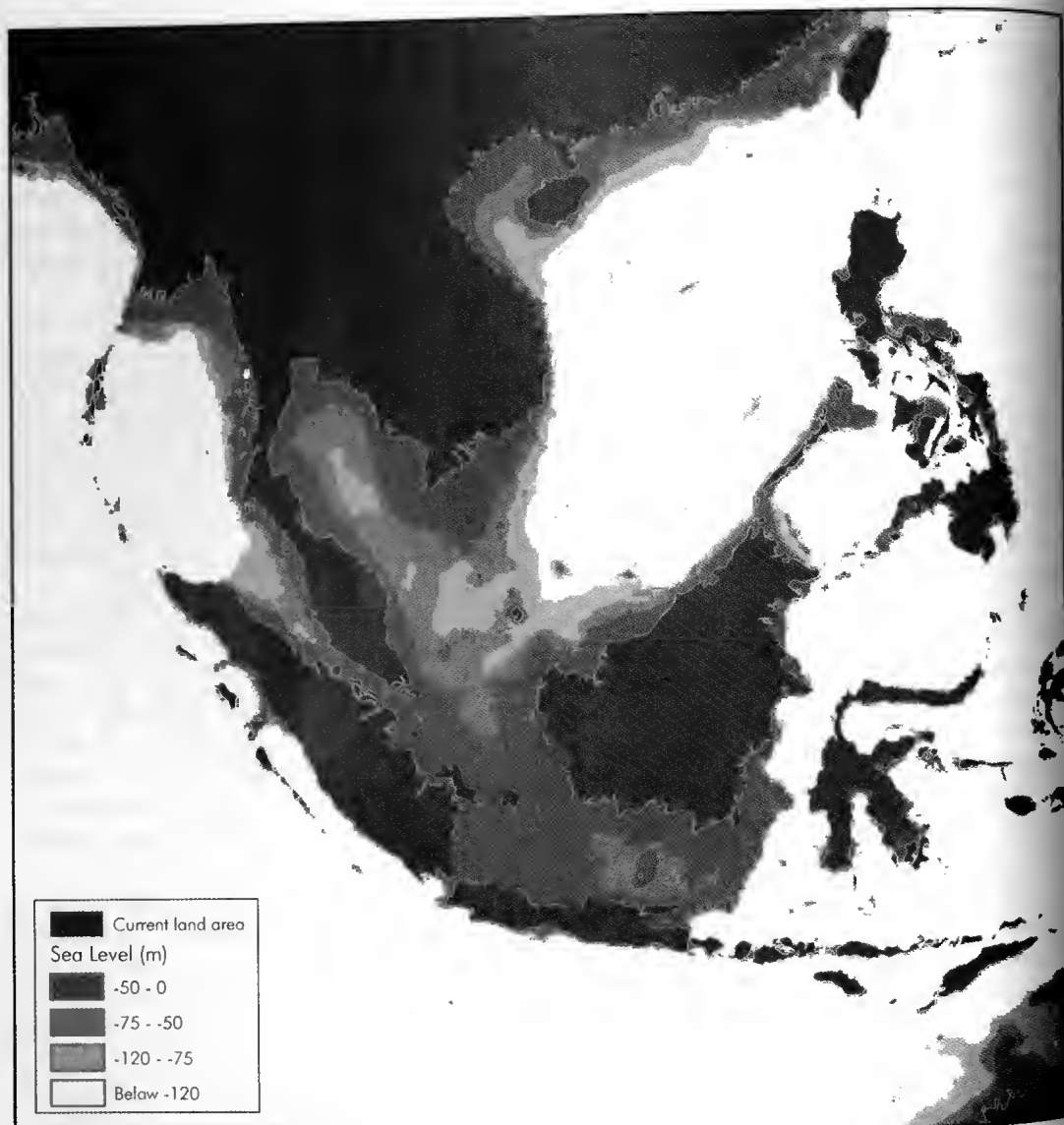


FIGURE 2. Map of Southeast Asia illustrating depth contours at 50, 75 and 120 m below current sea level. After Voris (2000). Reproduced with permission of the Field Museum of Natural History.

Broad biogeographic patterns reflecting these varied conditions have been identified and are frequently referenced when describing Vietnam's biodiversity (e.g., Eames et al. 2001; Hill 2000; Nguyen Nghia Thin and Harder 1996). Vidal (1960), Udvardy (1975), and MacKinnon (1997) have each defined biogeographic units within the Indochinese subdivision of the Indo-Malayan biogeographical realm. The most recent and detailed of these works places Vietnam at the convergence of four bio-units: Indochina (northwest and north-central Vietnam), South China (the northeast), Annamese Mountains (two regions in the central and southern Truong Son), and Coastal Indochina (the majority of central and southern Vietnam) (Fig. 3). Evolutionary and ecological evidence for these units is still being gathered. What evidence is there to date supporting these divisions and the

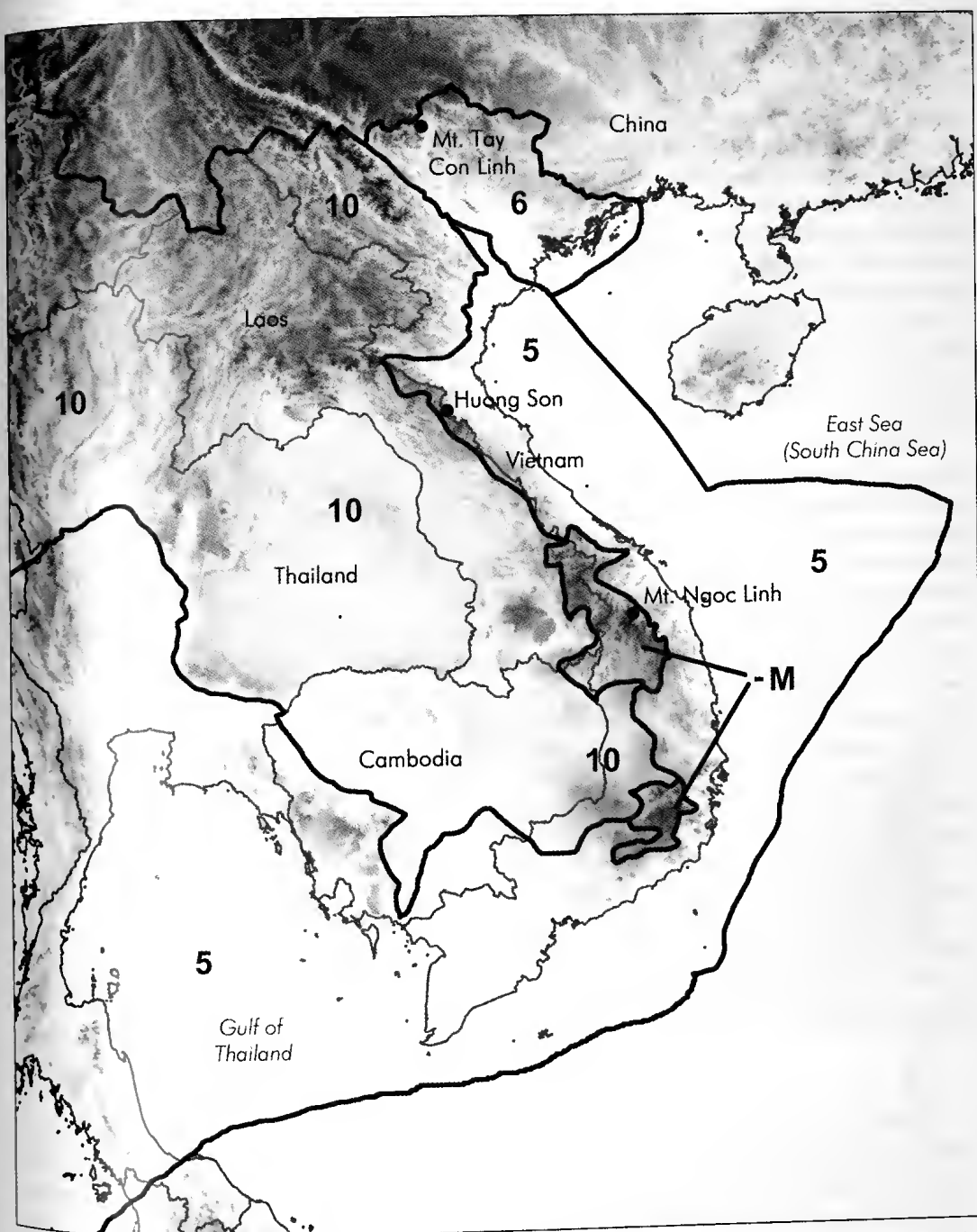


FIGURE 3. Map illustrating Vietnam's major bio-units (after MacKinnon 1997) and primary multi-taxon survey sites. The biogeographic units are: Coastal Indochina (Unit 5), Southern China (Unit 6), Indochina (Unit 10) and the Annamese Mountains (Unit -M). Study site localities were: Mt. Tay Con Linh, Cao Bo Commune, Vi Xuyen District, Ha Giang Province ($22^{\circ}46'N$, $104^{\circ}52'E$; surveyed 2000 and 2001); Rao An, Huang Son District, Ha Tinh Province ($18^{\circ}22'N$, $105^{\circ}13'E$; surveyed 1998 and 1999); and Mt. Ngoc Linh, Tra My District, Quang Nam Province ($15^{\circ}11'N$, $108^{\circ}02'E$; surveyed 1999).

specific roles of the region's geological and climatic history in shaping its biodiversity?

One supporting example comes from recent research in Vietnam and Laos. The ranges of the recently described Annamite striped rabbit (*Nesolagus timminsi*) and the newly rediscovered Heude's pig (*Sus bucculentus*) are both currently restricted to small areas of the northern Truong Son range bordering Laos and Vietnam. Their likely closest relatives, the Sumatran striped rabbit (*Nesolagus netscheri*) and the Javan warty pig (*Sus verrucosus*), respectively, live approximately 2500 km to the south, on the islands for which they are named (Groves et al. 1997; Surridge et al. 1999; Fig. 4). Genetic data suggest that the two rabbit species have been diverging for approximately eight million years (Surridge, et al. 1999). A similar pattern is seen in the distribution of Lovi's reed snake (*Calamaria loyii*) whose four subspecies are distributed allopatrically, one each in Vietnam's central Truong Son, Peninsular Malaysia, Java and Borneo (Darevsky and Orlov 1992). These may represent relict populations of formerly widespread ancestral species once connected by the emergent Sunda Shelf and isolated when seas rose and fell and forests expanded and contracted.

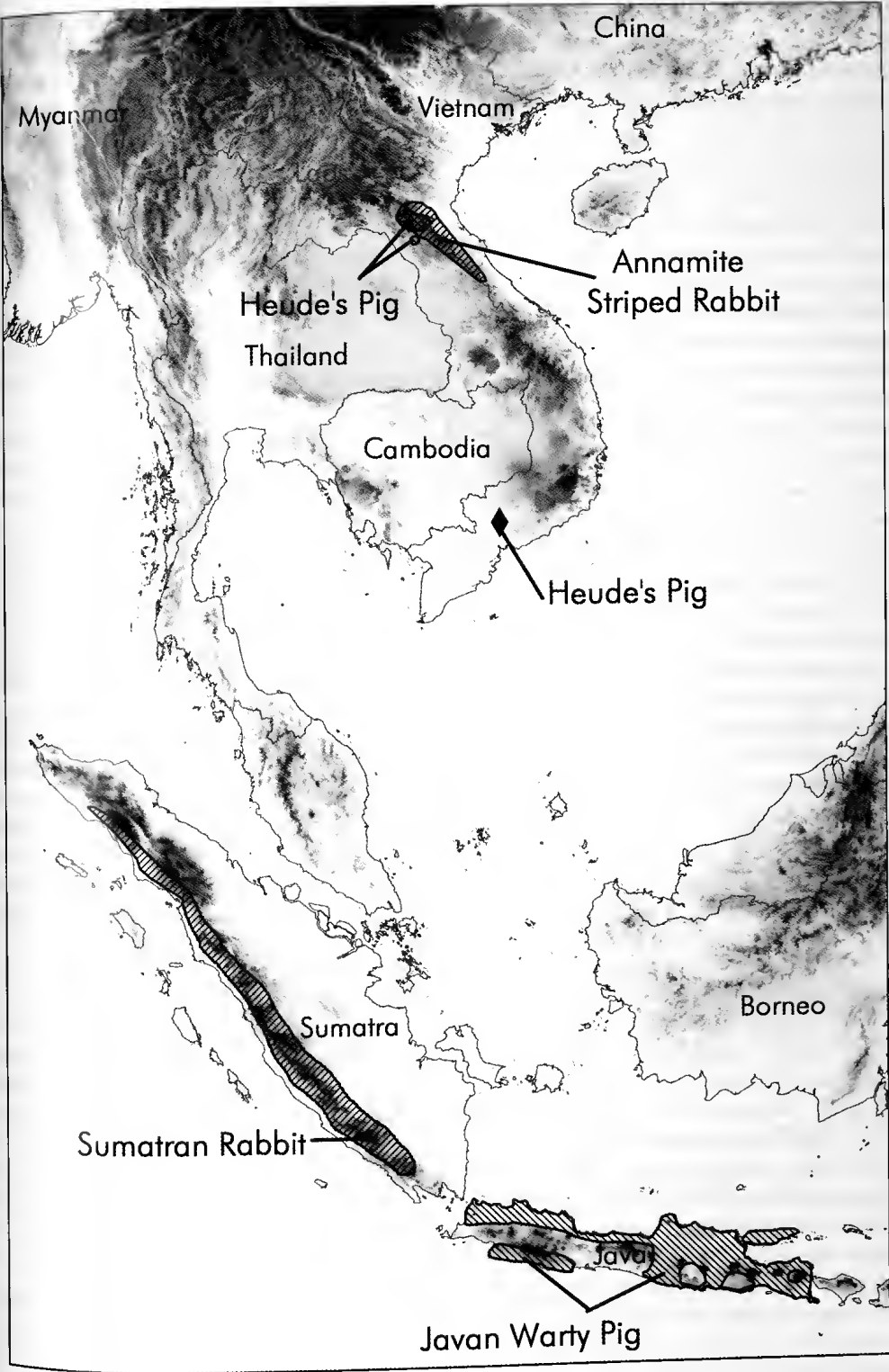
Within Indochina there is also a tentative suggestion that ancient climate fluctuations have influenced Vietnam's species diversity. Analyses of overlapping species distribution patterns in mainland Southeast Asia for a number of different taxonomic groups have led scientists to suggest that the Truong Son range served as a refugium for forest-dwelling species during cooler, drier times (Brandon-Jones 1996; Groves and Schaller 2000; Rabinowitz 1997; Surridge et al. 1999; Timmins and Trinh Viet Cuong 2001; but see Gathorne-Hardy, et al. 2002 for an alternative list of refugia). The refugium theory was first put forth to explain patterns of species richness in South America (Haffer 1969). In its initial formulation, the theory infers that observed diversity patterns stem from cycles of rainforest habitat contraction (forming refugia) and expansion that repeatedly isolate populations and lead to speciation events. Some scientists have challenged and revised this theory, suggesting instead that long-term climatic stability in refugia leads to high species diversity by facilitating both the evolution of recent 'neo'-endemics and the persistence of older "paleo"-endemics (Colinvaux et al. 2000; Fjelds  et al. 1999; Fjelds  and Lovett 1997). The two theories are not mutually exclusive.

The Kon Tum and Da Lat Plateaus of the Truong Son Range are both recognized as areas of high bird endemism, and the range is the home to three large mammal species considered relatively "primitive" members of their respective lineages (saola, Heude's pig, and the Annamite striped rabbit) (Flux 1990; Groves et al. 1997; Hassanin and Douzery 1999; Stattersfield et al. 1998; Tordoff et al. 2000). Elucidation of potential refugia in mainland Southeast Asia lies in future phylogenetic analyses of potentially informative taxa.

CURRENT CONSERVATION EFFORTS

Clearly, extensive research remains to be done on Vietnam's biodiversity and biogeography. This research has both theoretical and practical implications. Vietnam faces considerable challenges in attempting to conserve its rich and endemic biodiversity. Species distributions remain poorly known (as evidenced by the high number of rediscoveries), population data are lacking for almost all organisms, and ecosystem-level interactions are practically unknown. Vietnam harbors

FIGURE 4 (right). Map illustrating the historical ranges of the Sumatran rabbit (*Nesolagus netscheri*) and the Javan warty pig (*Sus verrucosus*) and the current known distributions of the Annamite striped rabbit (*Nesolagus timminsi*) and Heude's pig (*Sus bucculentus*). The two specimens on which the initial description of Heude's pig was based originated in southern Vietnam; it is unclear if these were collection localities or points of purchase. All ranges are approximations. Data from Dang N. Can, et al. (2001); Flux (1990); Groves and Schaller (2000); and Oliver (1993).



five of the world's 25 most endangered primates, four of which are endemic to the country and one, the grey-shanked douc (*Pygathrix nemaeus cinerea*), only described in 1997 (Conservation International 2002; Nadler 1997). Vietnam's rich biodiversity currently exists in a precarious and fragile state, and there are realistic fears that some of it will be lost before it is identified (Vo Quy and Le Thac Can 1994). Our understanding of Vietnam's diversity is burgeoning just as its species and ecosystems are facing increasing pressure brought on by the country's high human population (80 million people) and far-reaching political and economic changes.

In 1986, the government of the People's Republic of Vietnam initiated *Doi Moi*, heralding individual responsibility in agriculture and more encouragement of commerce (Werner and Bélanger 2002). The market economy has brought new levels of prosperity to Vietnam and made possible expanded rates of consumption. It has also created severe disparities of income. Vietnam now stands at a crossroads as it adjusts to an opening international market economy. The country's accelerating pace of development raises serious concerns for the minority populations and for the long-term prospects for the country's unique natural resources.

Current threats to Vietnam's biodiversity include direct exploitation through logging and hunting (both for subsistence and for national and international markets) and habitat degradation (Compton and Le Hai Quang 1998; DeKoninck 1996; Nguyen Nghia Bien 2001; Pham Binh Quyen and Truong Quang Hoc 2000; Poffenberger and Nguyen Huy Phon 1998). Habitat loss and degradation result from conversion of natural lands to agriculture (including the expansion of cash crops: Vietnam is now the world's second largest coffee exporter; Stein 2002), hydropower projects, urbanization and pollution (BirdLife International in Indochina 2003; Dudgeon 2000; Vo Tri Chung et al. 1998).

The Vietnamese government has a relatively long history of trying to address the problem of environmental degradation. In 1962, Ho Chi Minh established one of Vietnam's first protected areas, Cuc Phuong National Park. By 1990, the number of forest reserves had grown to 90, covering 1.3 million hectares (about 4% of the country). In 1995, The Ministry of Agriculture and Rural Development (MARD), the government arm charged with protected area development and administration, set a finite target of two million hectares for protection of forested areas (Birdlife International, 2001). The government simultaneously initiated a review of current and proposed protected areas aimed at removing degraded, non-forest lands from the current network and achieving equal representation of all Vietnam's habitats and associated biodiversity (Wege et al. 1999).

BIOGEOGRAPHY AND CONSERVATION RESEARCH

In an effort to contribute to Vietnam's restructuring of its protected area system, the Center for Biodiversity and Conservation at the American Museum of Natural History (CBC-AMNH) collaborated with a number of other organizations on multi-taxon surveys of currently unprotected forested areas in Vietnam. Collaborators included the Institute of Ecology and Biological Resources (Hanoi) (IEBR), Vietnam National University (Hanoi) (VNU), the Forest Inventory Protection Institute in the Ministry of Agriculture and Rural Development (Hanoi) (FIPI-MARD), Missouri Botanical Garden (MBG), World Wildlife Fund (WWF), and BirdLife International. Our goals were to survey three areas outside of the current protected area network to determine the diversity of plants and animals found in them, to identify cultural and subsistence uses of the areas for local populations, and to assess the conservation value of these areas in the context of both existing protected areas and additional proposed ones.

Study area selection was guided by a number of criteria. Areas had to be poorly known, forested, relatively undisturbed but still accessible for field work, and representative of biotic communi-

ties inadequately covered by the current protected areas network. We also used a biogeographic framework in combination with previous research to select areas potentially rich in biodiversity and ones where survey results could further elucidate the structure of diversity and its distribution in Vietnam. Our goal was to test two biogeographic hypotheses using survey results from study sites along north-south and east-west gradients: (1) the contributions of different biota (Sino-Himalayan, southern Chinese and Indo-Malayan) to regional diversity across the country, and (2) the existence of an endemic focus along the eastern flank of the Truong Son Range (Baltzer et al. 2001; MacKinnon 1997; Stattersfield et al. 1998; Timmins and Trinh Viet Cuong 2001). We also looked at elevation gradients to examine the relative roles of latitude and altitude in defining communities.

The most northerly site, Mt. Tay Con Linh in Ha Giang Province, lies in the South China bio-unit, east of the Red River and close to the Chinese border (Fig. 3). Habitats include submontane to montane evergreen and mixed deciduous evergreen forests typical of northern Vietnam's granitic mountains with a high diversity of conifers (Birdlife International 2001; Bain and Nguyen Quang Toruong 2004a; Harder, *in litt.* 2001). Vietnam west of the Red River has been better surveyed than the northeast (e.g., Bourret 1936, 1941, 1942; Delacour 1930; Delacour et al. 1928a; Delacour et al. 1928b; Eames and Ericson 1996; Osgood 1932); complementary efforts on the eastern side allow us to examine whether or not the Red River is an important barrier structuring diversity (Geissmann et al. 2000; MacKinnon 1997; Orlov et al. 2001). The most southern site, Mt. Ngoc Linh in Kon Tum Province, is part of the central Truong Son Range, a region known as the Western or Central Highlands, and it lies within the northern Annamese Mountain bio-unit (Fig. 3). Mountain plateaus in this region have elevated rates of endemism and BirdLife International has recently designated the Kon Tum Plateau an Endemic Bird Area (Vietnam's fourth) following the description of three new babbler species from it (Eames and Eames 2001; Eames et al. 1999a; Eames et al. 1999b; MacKinnon 1997; Tordoff et al. 2000). The forest sampled here is composed of low to medium montane broadleaf evergreens. The third site, Huong Son in Ha Tinh Province, lies roughly midway between the other two study areas in the northern Truong Son Range, within the Coastal Indochina bio-unit (Fig. 3). The low mountains in this area, which run along the Vietnam-Laos border, have been the site of some of the recent large mammal descriptions, e.g., saola (Vu Van Dung et al. 1993). The Huong Son study area encompassed lowland to lower montane broadleaf evergreen forests.

Researchers from the AMNH and collaborating institutions surveyed mammals, birds, amphibians, reptiles, freshwater fish, invertebrates and plants. At each of the major study sites, scientists sampled three to five locations along an elevation gradient. Whenever possible, workers on different taxonomic groups directly coordinated their sampling methods at each elevation. Taxon-specific sampling methods were employed with the general project goal of maximizing recorded diversity, including potentially undescribed species and species not yet known from the area. Collected specimens have been deposited at the AMNH, MBG, and IEBR. A detailed summary of study areas, methods, personnel, and results to date is available elsewhere (Hurley 2002).

Data from the 1998-2000 survey collections are still being analyzed, and most results remain preliminary. As with many other recent surveys, we collected previously undescribed species and recorded significant range extensions for both relatively well-known (e.g., Mrs. Gould's sunbird *Aethopyga gouldiae*) and recently described (e.g., an endemic glass snake *Ophisaurus sokolovi*) taxa. Notable descriptions (all in progress except the mammal) include a new shrew (*Chodsigoa caovansunga*), a new babbler (*Jabouilleia* sp.) and a minimum of four new anuran species (Bain and Nguyen Quang Truong 2004a, b; Lunde et al. 2003; Sweet and Vogel, in prep.; Vogel et al. 2003). Results from the 1999 amphibian collections at Mt. Ngoc Linh illustrate the potentially high

productivity of continued surveying in Vietnam. Of the 26 species recorded, 10 are restricted-range species, four represent range extensions of more than 200 kilometers for species endemic to Vietnam, two have been described as new and two more are currently being described (Bain and Nguyen Quang Truong 2004b; R. Bain, pers. commun. 2003; Hurley 2002).

Results are consistent with the hypothesis that there may be elevated rates of endemism in the central part of the Truong Son Range. As mentioned above, 10 (40%) of the amphibians collected at Mt. Ngoc Linh are currently known only from a small area, and the new taxa represent possible additional endemics (Bain and Nguyen Quang Truong, in prep.). The new babbler species, collected at the northern site (Mt. Tay Con Linh), necessitates a revision of the endemic Vietnamese genus *Jabouilleia*, types of which are known (currently as subspecies) from along the Truong Son Range (Sweet et al., in prep.). The likely result of these revisions is the elevation of one or more of these subspecies to the species level, adding to recorded endemism in the central Truong Son (Robson 2000). This revision may also contribute to understanding the regional evolutionary processes that have produced differentiation between Vietnam's central and northern avifauna. No additional, clear evidence of faunal endemism was found in the surveys of Huong Son in the northern Truong Son although the presence of three recently described and endemic mammals was recorded (Large-antlered muntjac, *Muntiacus vuquangensis*, saola, and Annamite striped rabbit) (Timmins and Trinh Viet Cuong 2001).

There is preliminary support for the contribution of biota from different biogeographical zones, although this varies with the geographic scale of the analyses. The two major biogeographic units intersecting in Vietnam are the northerly Sino-Himalayan and the southerly Indo-Malayan, with South Chinese influence in the northeast and endemic areas in the Truong Son Mountains (de Laubenfels, 1975; MacKinnon 1997). At a broad scale, collections from the northern (Huong Son) and southern (Mt. Ngoc Linh) Truong Son sites generally include elements of both major faunal groups whereas those from northeastern Vietnam (Mt. Tay Con Linh) show a strong affinity for the fauna of southern China.

At a smaller geographic scale, however, the results are less clear. One factor that disrupts these simple predictions of north-to-south diversity gradients is endemism. The presence of endemic species in the collections from Mt. Ngoc Linh adds a unique component to the fauna, reducing its similarity to the other two sites. For some taxonomic groups (frogs, gibbons) the Red River has been proposed to be a potentially significant geographic barrier, separating divergent eastern and western fauna in northern Vietnam (Geissmann et al. 2000; Orlov et al. 2001). If true, this has strong implications for conservation priorities and protected area designation in the region. Collections from Mt. Tay Con Linh in northeastern Vietnam support this hypothesis for some taxonomic groups but not for others. Insectivora species, collected during the small mammal surveys, include a number of species (e.g., *Scaptonyx fusicaudus*, *Blarinella griselda*) with stronger affinities to the fauna of southeastern China and Hainan Island than to the rest of Vietnam (Lunde, et al. 2003). However, both bird and amphibian and reptile surveys recorded a large number of range extensions across the Red River to northeastern Vietnam (Bain and Nguyen Quang Truong 2004a; Vogel et al. 2003). These results are not surprising as the newly recorded species fall within expected ranges, and they caution against assuming divergence between regions experiencing different surveying efforts. Our mixed evidence both supporting and refuting this hypothesis suggests that the taxonomic group being considered is an important consideration in the application of biogeographic theory to conservation.

Endemism and species distributions are important components in both biogeographic hypotheses and conservation decision-making. On a cautionary note, care should be taken in attributing full endemic status to new species as well as those known only from intensively surveyed areas. They

may represent "bastard endemics," species which, because of habitat loss or exploitation, now occupy only a subset of a formerly larger geographic range (e.g., the Indochinese Javan rhinoceros *Rhinoceros sondaicus annamiticus*) (Corbet and Hill 1992). Alternatively, they may be more widely distributed but not yet recorded from other areas because of undersurveying, because they were not previously recognized, or for both reasons.

Our experiences incorporating biogeographical information into conservation and biodiversity research have been positive. The surveying efforts were facilitated by our selection of study areas potentially high in species diversity and endemism and ones that might be informative in elucidating Vietnam's underlying patterns of diversity. Results from these surveys and analyses can inform conservation efforts, guiding decisions specifically about the current study areas and more broadly about other locations and communities in Vietnam. They also provide data for testing and refining biogeographical hypotheses, including the geographic and taxonomic scales at which they are applicable. These, in turn, can be used to refine and focus additional research and conservation efforts. An important component to continuing this natural history collections-based work is training and capacity building in Vietnam. Throughout the surveys, AMNH scientists provided equipment and training in standard field data collecting procedures and in the curation of the resulting collections to their counterparts at IEBR and university students. This work has already been productive: IEBR biologists used camera trapping to rediscover the hairy-nosed otter, *Lutra sumatrana*, in Vietnam, a Sundaic species thought to be extinct in Vietnam (Nguyen Xuan Dang, et al. 2000).

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Mission Possible: ALL Species Foundation and the Call for Discovery

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With approximately 1.7 million species currently named and as many as 9 to 99 million more to go, it is clear that there is a lot yet to be known about Earth's biodiversity. In 2000, the non-profit ALL Species Foundation was formed to call for the discovery, identification, and description of all the remaining species on Earth within one human generation — 25 years. ALL Species attracted proponents quickly and was embraced by the taxonomic community for its bold and audacious approach and the potential of new funding. ALL Species' global scientific endeavor is distributed on a wide geographical scale with diverse multinational participants. ALL Species endorses the principles and application of industrial business methods to biological inventory. ALL Species supports the knowledge of all species for all people. Unable to raise significant new funds for discovery, ALL Species reduced in 2002 to one staff member and shifted emphasis to promotion of tools and technology that accelerate the practice of taxonomy (e.g., digital imaging of type specimens, field-based microbiology equipment and molecular field sequencers, pattern recognition software, data rich identification keys, rapid publishing, and comparator tools). The mission? Possible.

The ALL Species Foundation began as an intellectual discussion among friends and rapidly grew into a project with the endorsement of approximately 100 prominent scientists from around the world. The mission: to accelerate the discovery of the planet's entire biodiversity in 25 years — one human generation.

WHAT IS ALL SPECIES?

ALL Species is a decentralized and non-bureaucratic global initiative, based on science-driven business models, and affiliated with entrepreneurial and catalytic scientists. Its purpose is to promote and accelerate the collection and systematic analysis of all biodiversity information and make it freely available on the internet.

HOW MANY SPECIES ARE OUT THERE?

Most scientists accept that about 1.7 million species have been named and described over the last 250 years, yet estimates of how many species exist on Earth vary from 10 to 100 million. The huge range between these last two numbers keenly demonstrates the immensity of the knowledge gap — we don't even know what we don't know.

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If we accept the fact that there are 6000–7000 practicing taxonomists describing two new species a year, the current rate of description is 15,000 per year. At this rate, describing 10 million new species will be completed in 2555. Obviously, a lot has to change to describe what remains within the timeframe challenge of ALL Species. For reasons outlined in this short paper, this rate of taxonomic discovery does not equate to the global significance of biodiversity.

WHAT ARE THE PRIORITIES OF SCIENTIFIC DISCOVERY TO BIOLOGISTS?

Most biologists believe the current extinction rate exceeds background and that Earth faces a “biodiversity crisis” due almost exclusively to human activities. This drives the imperative to know all species before many wink out of existence. Humans are a deeply curious species, but the dichotomy between our complacent acceptance of knowing only ten percent of life on Earth and our well-funded quest to discover life somewhere else in the universe is troubling. As far as we can tell, space is not under the same threat as Earth. Think about these incongruities:

- If you were sick with a life-threatening illness, would you want your physician to know only ten percent of the possible ways to save you; or possess only ten percent of the ability to diagnose what disease ails you?
- Would you hire an investment manager whose financial knowledge spectrum was only ten percent; someone who only read ten percent of the *Wall Street Journal*; someone whose advice was limited to a mere ten percent of the potential stock options available to you?
- What good is a library if you have access to only ten percent of what is there, whereas the remaining 90 percent is closed due to lack of funding; or even more disturbing, this resource is closed due to lack of use?
- What CEO of a corporation makes short-term or long-term buying, selling, or production decisions knowing only ten percent of its inventory or ten percent of its market? The life expectancy of a CEO in this position is highly endangered.

If enough energy and funds were dedicated to an Earth life search, ALL Species and its advisors believe the mission could be accomplished in 25 years. What if just a portion of the billions of dollars spent on SETI or NASA was redirected towards the search for life on Earth for the next 25 years? Many of the same creative scientists and engineers could be utilized to design sophisticated sampling robots for harsh earth environments, imaginative field- and lab-oriented tools for discovery, sequencing, and identification, and novel approaches to information analysis and storage.

WHY DOES KNOWING ALL SPECIES MATTER?

The impact of knowing all species, or most species at least, would be profound. Nearly every useful compound, food, fiber, or process used by humans was produced from either an idea inspired by observation of the natural world or by direct manipulation of some biological object or activity (Beattie and Ehrlich 2001). In the United States alone, 56 percent of the top 150 prescribed drugs is linked to discoveries made in the wild, yet less than one percent of the estimated 250,000 tropical plants has been screened for pharmacological properties (UNEP 2002).

Both biomimicry and nanotechnology are revolutionizing how we invent, compute, heal, harness energy, repair, conduct business, and feed the world. Research conducted at numerous labs around the world concentrates on the development of new products and materials derived from marine and terrestrial organisms. Some of these products or materials include new enzyme catalysts, novel bioadhesives, improved biosensors, optoelectric/catalytic and microelectronic devices, and microlaminate composites (Marine Biotechnology Center, University of California Santa

Barbara website). The discovery of more species equates to more models to observe and more sources to tap for scientific breakthroughs to improve the quality of life (Benyus 1997). Molecular level assays (receptor binding and enzyme inhibition) offer brand new perspective and potential for nature as a source of new pharmacologies (Verpoorte 2003).

Evolutionary biologists and ecologists have different perspectives than the average citizen about why knowing all species matters. From the scientific point of view, understanding biological mechanisms and evolutionary and ecological relationships is the best way to inform conservation and management decisions. This understanding is the best support for accurate priority setting and sustainable environmental policy. As E.O. Wilson says, knowing all species represents the true maturation of biology.

Actually, knowing all species ultimately represents long-term security for *Homo sapiens*. All agree that bio-security certainly has new meaning since 9/11. Pests and diseases are shared globally at an unprecedented level. Yet we know very little about species interactions that affect crop yields or the life cycles of vectors and the predators of vectors. Some believe that the most threatening crisis humanity faces is antibiotic-resistant bacteria in our own hospitals. However, it is significantly odd that the number of protist taxonomists remains very small relative to the number that study birds or plants.

WHY IS THE MISSION POSSIBLE NOW?

Many of the past impediments to global species discovery have been eliminated with modern advancements. Driven by Moore's Law, the continued exponential development of technologies and their decreasing cost over time provides the threshold for today's scientists to

TABLE 1. Some of the reasons why ALL Species advisors believe the mission is possible within the 25-year time frame

<i>Past Impediments</i>	<i>Current Solutions</i>
Travel difficulty	Advances in transportation
Glacial pace of information transfer	Internet
Access to collections/library	Online databases
Need to physically examine type specimens	Digital images reduce need
Delay/expense in publication	E-publishing
Limited compare/analyze tools	Rapid sequencing/Phylogenetics
Few experts	Capacity building initiatives

identify all life on Earth in their lifetime. Progress will be slow at first but once the inflection point of the curve occurs, momentum will gather speed. Table 1 lists some of the reasons why ALL Species advisors believe the mission is possible within the 25-year time frame.

WHAT HAS TO HAPPEN TO FIND ALL SPECIES?

For ALL Species' mission to succeed, societal changes must occur. National and international leadership must be demonstrated and pressure must be exerted upwards from the biological community about the value of taxonomy and the value of discovery. Barring a cautionary catastrophe that would inject a crisis mentality and jump start these changes, a critical fundament to the requirements is an abundance of 21st century thinking. Of course, the mission requires substantial funds, but almost more importantly it also requires:

- Evolution of the practice of taxonomy and systematics
- New tools, technologies, and training
- Unprecedented knowledge transfer to megadiverse countries

- A new corps of taxonomists
- Transformation of the culture within natural history sciences
- Increased public awareness

WHAT IS THE HISTORY AND CURRENT STATUS OF ALL SPECIES?

From its inception in 2000, ALL Species has seen itself as a neutral instigator and catalyst, a promoter and broker, and a fundraiser. After two international meetings in 2001 that framed the scope of the mission, advisory and governing boards were established. The advisory boards helped identify the first five-year goals that would either accelerate the process of taxonomy or provide testing ground for field inventory methods and protocols. These goals are listed in Table 2.

TABLE 2. The first five-year goals that would either accelerate the process of taxonomy or provide testing ground for field inventory methods and protocols

<i>First Five-Year Goals of ALL Species</i>
Image and web enable 50 percent of the primary type specimens
One global inventory of a taxonomic group
Quadruple the rate of species description
One comprehensive all-taxa biodiversity inventory
Increase the taxonomic capacity of developing nations twofold

Funding from The Schlinger Foundation in 2001 allowed the hiring of a small staff that set about forging partnerships and supporters to frame the discussion about how best to accomplish the mission. This staff also began creating tools to accelerate the business of taxonomy — such as a search engine. Within three months, this search engine <<http://www.speciestoolkit.org/index.jsp>> became the largest publicly available resource indexing a total of 873,979 species and 1,124,819 names. Full design and deployment of the Toolkit were put on hold in November 2002. However, the code is freely available under the GNU Public License at SourceForge at <<http://speciestoolkit.sourceforge.net/>> where the code and more extensive documentation are available. The ALL Species staff also designed and promoted a prototype Encyclopedia of Life — a consolidation of all biological information about species where every species has a web page and every web page is a portal to varying levels of biodiversity information about that species — from specimens to identification keys to experts to distribution maps.

ALL Species hosted one digital imaging workshop at the California Academy of Sciences during spring of 2002. From the success of that workshop, the E-Type and E-Description Initiative was launched — an effort to spearhead the digital imaging of primary type specimens and its original literature when possible. Through NSF supplemental funding, ALL Species co-hosted two E-Type Initiative Strategic Workshops at the Smithsonian (November 2002 and May 2003) where researchers from the major collections in the United States and Europe and the developing world discussed the benefits and goals of the Initiative and mapped preliminary strategies for the Initiative and for specific taxon groups.

Unable to raise significant additional funds for the young organization with big ideas, ALL Species was reconfigured in late 2002. Hoping to keep the mission alive until a more auspicious economic climate, four institutions stepped forward to provide support for one staff person to concentrate on the E-Type and E-Description Initiative and other ALL Species activities through 2003 and possibly into 2004: California Academy of Sciences, Field Museum, Missouri Botanical Gardens, and Museum of Comparative Zoology — Harvard. ALL Species' advisory boards remain active on a volunteer basis.

As of June 2003, ALL Species had met with considerable success on at least two of these first goals. Through Conservation International, a one-year all-taxa biodiversity inventory is slated to

occur in Los Amigos, Peru following protocols and methodologies designed by Terry Erwin of the Smithsonian (former ALL Species Science Chair). At the instigation and urging of ALL Species, in 2002 the National Science Foundation launched a brand new \$14 million program called Planetary Biodiversity Inventories (PBI) to support the global inventory of major taxonomic groups. The first four awards will cover catfish, eumycetozoans (slime molds), solanum (nightshade family of plants), and plant bugs. Even in its reduced state, ALL Species was able to contribute \$25,000 to the PBI effort.

IS THE MISSION POSSIBLE?

Every biologist needs to be part of this mission whether they are an ALL Species advisor, a previously quiet supporter at the sidelines, or someone reading this text by accident. We all need to promote the need to know. Each of us needs to take every opportunity wherever we can to stress the value of discovery and the value of knowing, and to broadcast the importance of taxonomy and taxonomic products to society. Useful new tools and developments that accelerate the practice of taxonomy need to be fostered and promoted. In short, ALL Species challenges each of us to become biodiversity diplomats. We need to coordinate across disciplines and to collaborate at new levels. We need to speak up and speak out and to mobilize. Is the mission possible?

Only if we each follow Mahatma Gandhi's advice and "Be the change you wish to see in the world."

UPDATE: AUGUST 2004

Unfortunately and anticlimactically, ALL Species is currently without staff and the foundation is dormant. Attempts over the past six months to find an organization in the mutually strategic position to adapt the assets of ALL Species have been unsuccessful. The good news is that E-typing is far more common and the Smithsonian's new Encyclopedia of Life will take ALL Species' and E.O. Wilson's idea of a web page for every species and try to make it happen.

So, the vision will continue, for after ALL, vision is what makes any mission possible.

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New Pangea: Homogenizing the Future Biosphere

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The literature discussing future human impacts on the biosphere has tended to focus on the metaphor of the next (sixth) mass extinction. I outline some benefits of another metaphor, that of the New Pangea. Conceptualizing human impacts in this way not only emphasizes the inevitable loss of global biodiversity but also includes the loss of regional diversity that occurs through homogenization, when unique native species are replaced by a relatively limited pool of widespread exotic species. The New Pangea metaphor thus emphasizes not only the “losers” of the next extinction but also the “winners”, those species that will inevitably thrive. This metaphor specifies how human impacts are operating to alter the biosphere because biotic homogenization is a two-step process consisting of human-accelerated: (1) long-distance dispersal including removal of barriers; and (2) replacement of diverse natural habitats with a much smaller diversity of human-dominated habitats that will support a smaller global diversity of species. The process is enhanced even more by the highly selective nature of human transport and habitat creations so that species from certain groups disproportionately become winners or losers. The ultimate outcome will likely be a superhomogenized biosphere, with biotic intermixing on a scale far greater than any time in Earth’s history. Conservation efforts to slow down the extensive species intermixing will be impeded by the fact that exotic species often increase species richness and spatial diversity (species turnover) at local scales. The general public and their policymakers, who typically perceive the world only at local scales and often value exotic species for crops, pets and many other utilitarian reasons must be educated about the global and long-term consequences of biotic exchanges.

Comparison of current human impacts on the biosphere to diversity patterns in the fossil record is essential for conservation biology (Purvis et al. 2000a, 2000b). Without some kind of natural baseline, it is impossible to understand the radical changes being made to our current biosphere by humans. Examples of crucial baseline parameters include extinction rates, rates of biotic interchange, extinction selectivity (which taxa are more extinction-prone) during background and mass extinctions, and recovery patterns following mass extinctions (Jablonski 2001).

However, an important message of the fossil record is that it is often difficult to generalize about these baseline parameters (Woodruff 2001). One reason is that the sheer complexity of the biosphere does not make it easy to find simple rules. Increasing this complexity is that the drastic and rapid changes being wrought by humans are probably even more rapid, unique and varied than any physical changes that have occurred in geological history (Western 2001). Still other obstacles to fossil versus modern comparisons are pragmatic, such as the practical difficulty of measuring extinction rates now or in the past (Regan et al. 2001).

Despite these problems, there is a substantial literature relating modern extinctions to the fos-

sil record. Perusal of this literature reveals two major metaphors that have emerged. One is that of the Sixth Mass Extinction (Leakey and Lewin 1995; Pimm and Brooks 2000), which relates the impending biotic crisis to the previous five global catastrophes that eliminated a large proportion of species. The second metaphor is the New Pangea (Rosenzweig 2001a, 2001b), which relates the impending crisis to the biotic reorganizations that occurred during the assembly of the Pangea supercontinent in the late Paleozoic Era.

In this paper, I discuss the New Pangea metaphor, and some of its advantages. Unless humans disappear, the impending biotic crisis will apparently be a prolonged one. The Sixth Mass Extinction metaphor implies that the impending crisis is some kind of single event. Also, the New Pangea metaphor focuses on both winners and losers of global environmental change. Extinction is nearly always selective (McKinney 1997) with some groups being selectively removed whereas other groups selectively benefit (McKinney and Lockwood 1999). In discussing a New Pangea, it is possible to conceptualize certain groups as beneficiaries. The Sixth Mass Extinction emphasizes only one side of this ledger, the losers. A final advantage of the New Pangea metaphor is its explicitly geographic component. As Jablonski (2001) noted, considerations of the current biotic crisis need to incorporate the reality that extinction rates now vary substantially among regions, just as they often have in the past. The New Pangea metaphor includes this, by noting that the winners of the impending global changes will tend to undergo geographic range expansion, replacing the losers whose ranges will shrink or disappear.

Like most metaphors, the New Pangea one is not perfect, and it certainly is not my own idea. Pangea is not a perfect metaphor for the future biosphere in part because the end-Permian mass extinction resulted from a combination of many factors, of which continental assembly was only one (Erwin 1993). In addition, human alterations of the biosphere are so rapid and are occurring in so many ways that any comparison with the comparatively simple natural dynamics of the past must be considered as speculative.

To my knowledge, Rosenzweig (2001a, 2001b) was the first to use this metaphor in its current context, although Brown (1995) reviews some very relevant species-area calculations predicting biotic homogenization from the removal of geographic barriers. Also, several related allusions to the future homogenized biosphere have acquired some currency in the literature. The term "Homogocene" has made its appearance in several places (e.g., Guerrant 1992) to describe the next geologic epoch. David Quammen (1998) has labeled the future biosphere as the "planet of weeds". Although this latter metaphor is certainly colorful, I suggest that the New Pangea concept is more informative because future winners of the human-dominated biosphere will consist of more than only "weedy" species, most notably pets, ornamental plants and other species that we cultivate for our own uses. The Pangea concept also conveys much about the processes that will shape our future biosphere.

NEW PANGAEA: TRANSPORTATION PLUS INCREASING HABITAT UNIFORMITY

The extinction of local native species and their replacement with widespread species from another locality are ongoing processes that promote biotic homogenization (Olden and Poff 2003; Olden et al. 2004). The mixing process has only just begun but its effects are visible to anyone who travels very far, especially to islands, where biotic homogenization is most apparent in such groups as birds (Harrison 1993) and snails (Cowie 2001).

Homogenization is probably an inevitable trend of a globalized modern world, occurring with culture and technology as well. Commentators in several fields of study often note the increasing uniformity of the world by the loss of local and regional distinctiveness (Quammen 1998; Western

2001; Olden et al. 2004). In the social realm of economics and culture there is growing concern over "globalization," whereby the wide diversity of the world's cultures is becoming replaced by a globalized mass culture (Goldsmith and Mander 2001).

Although humans are obviously not forcing the continents together, we are recreating many of the major conditions found in ancient Pangea that promoted species mixing. Specifically, modern species mixing is promoted by two distinct steps: increasing dispersal and the spread of habitat uniformity. In the past, increased dispersal occurred by the removal of barriers. Now, humans not only remove barriers (e.g., the Panama Canal) but we also accidentally or intentionally transport species all over the globe.

The second step in the mixing process, habitat uniformity, is perhaps less obvious and is given less discussion in the scientific literature on species mixing. But this second step is very important because any species immigrating into an area cannot become established unless the area provides suitable habitat. In the future, the widespread creation of human-dominated habitats, such as cities and farmland, will provide the habitat used by introduced species (Woodruff 2001, and see below).

It is commonly noted that current extinction rates are orders of magnitude higher than those of the past (Woodruff 2001). In contrast, I know of no one who has compared rates of exotic species introductions to biotic exchanges in the past. Clearly, this is a difficult comparison to make, especially in light of our lack of knowledge of current species introductions in the marine realm where fossil data are most complete. However, what we do know about marine introductions from the global shipping industry (Ruiz et al. 2000) makes it evident that current rates of introduction are very high, on the order of hundreds of species introductions per year for most large geographic regions, and probably increasing exponentially.

Thus, as with extinctions, modern introductions are orders of magnitude higher than natural background rates, and they probably also exceed introduction rates even during past natural catastrophic episodes. In other words, rates of biotic homogenization are also orders of magnitude higher than at any time in earth's history. This is because of the high rate of dispersal (transportation) plus the high rate of habitat creation for exotic species. Ultimately, for reasons I discuss next, the overall extent of homogenization also seems likely to exceed that of the past.

SUPERHOMOGENIZATION: CREATING WIDESPREAD HABITAT FOR A FEW NEWCOMERS

Most human activities transform natural ecosystems in ways that reduce habitat for native species, and create habitat for nonnative species (Williamson 1996). There are many examples, so I will focus on three of the most obvious and widespread activities: urbanization, pollution, and other "disturbances" and cultivation.

Urbanization is one of the fastest-growing causes of habitat loss for native species (McKinney 2002). To the frequent traveler, homogenization is probably most visible in the increasing physical sameness of cities of the world. As James Kunstler (1995) describes so well in his popular book, *The Geography of Nowhere*, the rise of modern industry in the 1800's was accompanied by the spread of advanced technologies, such as steel-reinforced concrete, that allowed the construction of skyscrapers to house increasing numbers of people. Although they may differ in stylistic details, large office buildings tend to converge in their appearance. Kunstler (1995) also describes the post-World War II mass production of suburban housing subdivisions in the United States. Since 1945 American suburban housing has become dominated by development corporations that buy large parcels of land that are subdivided into small plots for houses based on a very small number of basic design schemes.

This widespread physical uniformity promoted by urbanization is accompanied by an increase

in biological uniformity. For example, well over 50% of the plant species found in most major cities around the world are not native to the region where the city is located (Pysek 1998). Similarly, urban-rural gradient studies show that the proportion of exotic species increases from the countryside to reach a peak in the highly urbanized downtown areas. This pattern has been documented for many groups, including plants, birds, mammals, and insects (Blair 2001; McKinney 2002). As a result, synanthropic species, well adapted to intensively urbanized city areas, are among the widespread and homogenized biota in the world (Johnston 2001).

Another kind of widespread habitat change would include pollution and many other ways that humans degrade natural ecosystems. Extreme pollution of air, water, and land often degrades those media to the point that only a few nonnative species are able to tolerate habitats in them. An example would be carp and other freshwater fishes adapted to polluted waters (Rahel 2002). Similarly, fragmentation of forests by logging, roads and human settlements increases the exotic plant invasion rate (MacQuarrie and Lacroix 2003).

Finally, cultivation of species is a major mechanism of homogenization. Monocultures for food, timber and many other plant products are increasingly widespread in many parts of the world. Examples where homogenization by these activities has been discussed would include coffee plantations (Marcano-Vega et al. 2002) and agricultural land use in Puerto Rico (Grau et al. 2001).

MEASURING BIOTIC HOMOGENIZATION

Despite the increasing biotic homogenization caused by human activities, there have been surprisingly few attempts to study, and especially measure it. In those few studies where biological homogenization is actually measured (e.g., Rahel 2000, 2002; Blair 2001), the most common method is Jaccard's similarity index. This index measures the proportion of species that are shared between two locations:

$$\text{Jaccard's Index (JI)} = c/(a + b + c)$$

where c = number of species in common to both locations, a = number of species only found at site a, and b = number of species only found at site b. JI can vary between 1 (all species shared) to 0 (no species shared) between the two locations.

A basic null hypothesis for homogenization studies to test is that humans should generally increase Jaccard's Index, or similarity of species among locations. When humans remove unique native species, we increase JI by decreasing a and b in the denominator. Conversely, when we add widespread non-native species that are shared between both locations, we increase the numerator. For example, using Jaccard's Index, Rahel (2000, 2002) found that the fish faunas of states in the U.S. have become more similar, largely because of introductions of game fishes plus the widespread alteration of aquatic habitats from dams, dredging and many other human activities. A similar pattern was found by Marchetti and others (2001) for fishes in California. They demonstrated that the JI increased through time, as humans increasingly modified water bodies. I found the same pattern with plants among various locations in the United States, where increasing species richness of exotics tended to increase the JI (McKinney 2004).

We might expect that, as humans increasingly modify environments, we should find increasing similarity among these modified locations. The most intensively altered environments, such as highly urbanized areas, should thus show the greatest amount of homogenization. Evidence for this has been especially well documented by biologists studying birds. Blair (2001), for example, used Jaccard's Index to show that the birds of downtown Palo Alto, California are relatively similar to

the birds of downtown Oxford, Ohio. In contrast, when he compared the birds living in the natural environments outside those cities, they were very dissimilar (Blair 2001).

In addition to similarity indices such as Jaccard's Index, another way to measure homogenization is the species-area curve. Rosenzweig (2001a, 2001b) discusses how the slope of the species-area curve tends to be higher when sampling areas with many unique species, such as islands, mountains, or highly diverse tropical rainforests. Conversely, as humans homogenize islands, and all other habitats, new species will accumulate more slowly on species-area curves because locally unique species are lost and more species are shared among areas. In other words, homogenization tends to lower the slope of the species-area curve. This was found, for example, by Flather (1996) when comparing curves of bird species in intensively farmed regions of the United States (which are very homogenized) versus bird species in more natural areas of the United States. In his book *Macroecology*, James Brown (1995) uses species-area patterns to predict that between 35–70% of species now on Earth will disappear if humans completely homogenize the global biota. I used this method to predict the loss and homogenization of marine species from the building of the Panama Canal, and concluded that it seems to be fairly accurate (McKinney 1998).

I hasten to add that the species-area method to predict species homogenization is fraught with many problems and assumptions. These problems have been discussed at length by Collins and others (2002) and they make a persuasive case that such predictions are very tentative. However, the species-area curve is well known, and it is a good way to at least conceptually visualize how homogenization affects large-scale patterns, especially where such complexities as habitat diversity are also factored in.

Thus far, I have focused on measuring homogenization as the number of shared elements. Jaccard's Index measures the number of shared species between ecosystems, and the species-area curve tabulates species accumulation along a sampling gradient. One important limitation on this method is that it assumes that the elements counted are individual and distinctive units. But many of these elements can be blended with one another. Cultural items including architectural styles and languages, for instance, are often blended, as evidenced by such dialects as Creole. This is also true of biological homogenization, where distinct but related species can sometimes interbreed when exotic species are introduced.

Sometimes called "genetic or biological pollution," this genetic intermixing between native and a related introduced species has become increasingly common (Petit 2004). Many examples are documented in a review by Rhymer and Simberloff (1996). Some of the more familiar examples would include the genetic mixing of many introduced crop plants with their wild relatives. Among animals, mallard ducks (often introduced for hunting) are infamous for interbreeding with native ducks. For instance, hybridization with introduced mallards has contributed to the decline of the endangered, endemic Hawaiian duck. Mating with feral housecats has contributed to the genetic decline among several species of wildcats native to Africa and Europe, and the bobcat of North America. A similar decline has occurred among several native wild species of canids, through interbreeding with domesticated dogs. Examples include many populations of wolves. In Europe, what had been considered pure wolf (*Canis lupus*) populations have turned out to be largely hybrids between wolves and domestic and feral dogs (*Canis familiaris*). Genetic blending among species not only dilutes the gene pool of native species and subspecies, it also affects the evolutionary process (Olden et al. 2004).

Even if we set aside the problem of blending among elements, a more thorough measurement of homogenization requires that we look beyond tabulating the number of elements (such as species, architectural styles, or languages) that are shared. We also should try to examine the relative abundance of each element where we can. For example, suppose we compare two cities and

find that they share all ten species of non-native birds in them. But what if all ten species are very common in one city and they are all very rare in another? We might not even see the birds in the city where they are rare. In other words, the similarity among cities is even greater where species are not only shared, but where each species has similar abundances in each city. Ecologists have the ability to incorporate abundance data into such comparisons by using the Bray-Curtis and several other indices (Waite 2000). However, I am not aware of any studies of homogenization that have included abundance data thus far.

In addition to homogenization from the exchange of species and genes, we should also consider other ways that the biosphere is becoming more uniform. Olden and others (2004), for instance, have noted the potential importance of functional homogenization. This examines the increasing similarity among human-disturbed ecosystems in such community traits as energy flow, food web structure and complexity, and chemical cycles. These new homogenizing human-dominated ecosystems tend to be more simplified than natural ones (Western 2001). From an energy perspective, one may see this as a process whereby the few species that can exploit sources of food increasingly provided by human activities become widespread. Examples include species that exploit cultivated plant communities such as crops or suburban ornamental plants, and species that thrive on garbage, bird seed and other forms of imported foods. In many cases, these "subsidized" species attain population densities far above their natural abundance, such as documented in coyotes of southern California (Fedriani et al. 2001).

THE CONSERVATION CHALLENGE OF LOCAL DIVERSITY BUT GLOBAL MONOTONY

An important consequence of biotic exchanges in the past is that they sometimes have led to increases in local and regional diversity (Vermeij 1991). This is also often true today, as human activities increase the number of species in an area. Sax and Gaines (2003) have reviewed the literature to document such local and regional increases produced by exotic species for many groups, especially plants and freshwater fishes. In such cases, the number of exotic species gained exceeds the number of native species that become extinct (Mooney and Cleland, 2001; Rosenzweig, 2001a, 2001b). A main explanation for this species enrichment is that increasing modification of the environment not only degrades habitats of native species but also creates a diversity of habitats for many exotic species that are imported by humans (Sax et al. 2002). Cities, for example, often have a greater richness of plant species than surrounding areas for this reason (Pysek 1998) because cities have a rich variety of land-use and habitat mosaics (McKinney 2002). Similarly, suburban landscapes are very rich in lawn grasses, shrubs, flowers and trees that are cultivated by homeowners (Hope et al. 2003).

The problem for biodiversity conservation is that despite these local species enrichments, global biodiversity continues to decline. Furthermore, because these locally diverse exotic species are typically widespread species, there is a global trend of increasing homogenization (Rosenzweig 2001a, 2001b). Harrison (1993) documented this process on Pacific islands. She showed that the extinction of native birds by exotic birds introduced by humans has increased the net local (alpha) bird diversity on those islands. However, the total regional bird diversity of those islands has declined because the introduced birds tend to be the same species that are shared among many islands. From a genetic perspective (Petit 2004), this process represents the loss of unique genes and genomes which are replaced by more common ones.

This pattern of local enrichment but global decline is a crucial one for conservation biology because it may divert public attention away from the more global problem of global species decline. The general public, and most policymakers, tend to think mainly at local scales (Ornstein

and Ehrlich 1989). This is illustrated by the fact that, although people often value species diversity, most of the general public cannot identify whether a local species is exotic (McKinney 2002) and, even when they do know it is exotic, they still place a high value on that species if it is aesthetically pleasing (Reichard and White 2001), good for sport or has some other utilitarian value (Brown et al. 1979; McKinney 2002).

ENHANCING HOMOGENIZATION: WINNERS AND LOSERS ARE CLUMPED IN GROUPS

Extinction is almost never random. Ecologists and paleontologists have accumulated a large literature documenting how certain traits make some species more prone to extinction (McKinney 1997, Purvis et al. 2000a, 2000b). In general, these traits are correlated with a higher risk of extinction in the past, and in today's human-dominated world. Examples of such extinction-promoting traits include: low abundance, large body size, slow reproduction, specialization (such as a specialized diet or habitat), and adaptation to island life.

In addition, traits such as body size and reproductive rate tend to be shared by closely related species so that some phylogenetic and taxonomic groups tend to contain more species at risk (McKinney 1997; Purvis et al. 2000a, 2000b). Birds are among the best studied in this respect. For instance, Lockwood and others (2000) found that certain bird families, including the pigeon family and the parrot family, have a higher concentration of globally threatened species than would be expected if globally threatened bird species were randomly distributed among families. In accord with the extinction-biasing traits noted above, pigeons and parrots tend to be large and slowly reproducing birds. In addition, they are also often harvested for food and pets. In contrast, the woodpecker family has fewer threatened species than expected. Similarly, a study of threatened vertebrates of the United States showed that threatened species of mammals, birds, reptiles, amphibians and fishes tended to be concentrated within certain genera (Lockwood et al. 2002). This concentration of species losses in certain groups can accelerate biodiversity loss, essentially by disproportionately pruning certain branches on the phylogenetic tree (Purvis et al., 2000a, 2000b).

The concentrated loss of species also can enhance biological homogenization. By removing species that belong to unique groups, biological communities lose their most distinguishing elements. Homogenization is enhanced if those species that expand their geographic ranges (the winners) are not randomly distributed among groups but are concentrated within the same few groups. For example, Lockwood (1999) found that bird species purposely introduced and established by humans are not randomly distributed among families but have been concentrated in certain families. The duck and pheasant families are examples. In their case, these species have been mainly introduced for their value as game birds. Aside from human preference (such as sport for game birds), another key reason for clumping is that species in certain groups have, by evolutionary chance, evolved adaptations for exploiting the kinds of habitats that humans often create. Species in the grass family, for example, tend to be well adapted as weeds and have often spread widely for that reason (Daehler 1998). Among insects, flies and beetles (among others) seem to be overrepresented (Vazquez and Simberloff 2001).

The important outcome is that humans not only replace locally unique species with the same few species, but those same few species tend to be from the same few taxonomic groups, such as the duck family (among birds) and the grass family (among plants). Clumping enhances homogenization because our biota not only consists of the same few species, but, because they are from the same few groups, even these few tend to be similar to one another (McKinney and Lockwood 1999).

Clumping is not limited to taxonomic groupings. Winners and losers are often nonrandomly distributed among ecological groupings as well. Species adapted to the forest edge and species that are generalists and have a broad diet, for example, are often favored in human-dominated environments (McKinney and Lockwood 1999; Western 2001). Again, this enhances homogenization because the world becomes dominated by species in these categories.

CONCLUSIONS: HOW BLENDED THE FUTURE BIOSPHERE?

How far will the mixing process go in the future? Efforts to answer this are impaired by the lack of study of homogenization. Most of the few homogenization studies thus far have analyzed freshwater fishes, perhaps because this group has experienced some of the most extensive homogenization of all groups. These studies include fishes in the United States (Radomski and Goeman 1995; Rahel 2000, 2002; Marchetti et al. 2001; Scott and Helfman 2001) and in the state of Tennessee (Duncan and Lockwood 2001). In addition, homogenization has been studied in Pacific island snails (Cowie 2001), Pacific island birds (Harrison 1993) and urban birds in the United States (Blair 2001). McKinney (2004) found that exotic species increase homogenization among North America flora. The main metric of homogenization in all these studies has been to compare the species composition of communities before and after human disturbance and the introduction of exotics. In all cases, these studies conclude that human activities have significantly increased the amount of homogenization by increasing the proportion of shared species among human-disturbed communities.

It seems likely that homogenization will continue for many decades and will eventually produce a biosphere that is more homogenized than any in Earth's history. In the first place, there is enormous potential for species movement in today's world, with modes of transportation that can easily leapfrog over all natural barriers. In the second place, there is a greater potential in today's Pangea for homogenization of the physical environment. As humans destroy unique natural environments, they tend to replace them with the same types of artificial environments throughout the world. For reasons of efficiency and human tastes, cities, farms, roads, airports, and most other human environments tend to have much more in common with similar human environments elsewhere in the world than with their original natural environment. In the third place, human selectivity, by concentrating the winners and losers of the next mass extinction into certain higher taxa and ecological categories (e.g., early successional species), will likely enhance homogenization.

Will the entire biosphere ultimately become completely and uniformly homogenized? It seems unlikely. Natural limits on species ranges include physical geographic gradients such as climate and soil. For example, one can speculate that the tropical South American exotic species that now thrive in the cities of South Florida will probably not persist in the cities of Canada. Human-imposed limits to homogenization may also exist. Conscious efforts to reduce native species extinction, non-native species transport and establishment, and many other conservation efforts could, in theory, curb the ultimate extent of biological homogenization.

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Twenty-First Century Systematics and the Human Predicament

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Systematists could play an important role in preserving biodiversity, but for the most part they have not yet done so. By creating a 21st century systematics with one major focus on that task, not only would humanity be benefited, but taxonomy itself could regain some stature among the biological sciences. Necessary steps to create such a systematics include developing methods of dealing with population diversity, concentrating effort on model groups and using them to investigate mechanisms of population differentiation, and designing a biodiversity database to answer important and interesting questions. Systematists should stop writing about the long-solved "problem" of "what is a species?" and abandon impractical plans for creating a cladistic tree of all life forms — a project that, even if it could be completed, would yield little of value. Taxonomists, like all other scientists, should be trained to sample nature in order to understand it. Systematics should be expanding its boundaries and collaborating with scientists in many other disciplines, where its knowledge and techniques can make valuable contributions to solving human problems.

The stuff we taxonomists study is disappearing at a rate unprecedented since a comet sent the non-feathered dinosaurs packing some 65 million years ago (e.g., Thomas et al. 2004). At the same time, never has the need for good systematics been more obvious and excitement in parts of the discipline more palpable. The time has come to build on that. Humanity is, after all, faced with the degradation of a crucial component of its natural capital, the populations and species that comprise biodiversity and are working parts of its life-support systems (Daily 1997). The "human predicament" is the expansion of humanity's impacts on those systems to the point where both the long-term biophysical sustainability and the socio-political stability of society are seriously threatened (Ehrlich 2000; Ehrlich and Ehrlich 1991, 2004). Perhaps the biggest challenge in achieving global sustainability that systematists and other scientists face today is finding novel ways of preserving our natural capital, especially biodiversity (e.g., Daily and Ellison 2002). By vigorously taking up that challenge, we can simultaneously create a 21st century systematics with expanded horizons, add a series of exciting problems to our research agenda, expand our collaboration with other scientists, and gain more financial and moral support for our core activities.

And why shouldn't we? After all, biodiversity is the natural domain and subject of investigation of systematics. To me, the core of systematics is the description of the past and present diversity of life (including the diversity of behaviors and interactions) and the classification of life forms, along with the development of tools for communicating about that diversity to other scientists and to the general public. Moving out from that core, systematists should naturally be concerned with, and do research on, the mechanisms that generate biodiversity and cause lineages to change through time, that create biogeographic patterns, and that cause diversity to increase or decline. That is, systematics blends at the edges with evolution, ecology, behavior, and conservation biology.

So it seems appropriate to ask why our discipline has had so little impact on public policy, even though some of the leaders in the fight to save biodiversity, for instance Peter Raven and Ed Wilson, have been systematists. Why is the general attitude toward systematics that was summarized by a journalist in the *Baltimore Sun*, in the context of a fascinating taxonomic discovery: "Today it's a backwater, ignored by students and patrons of science in favor of genetics and other cutting edge careers" (Stroh 2003)? Why, equally, has the new discipline of conservation biology been largely "captured" by ecologists, when that discipline could just as logically have been allied with systematics? Systematists are in the best position to measure what is disappearing and what is at risk; ecologists are well placed to figure out what environmental changes are causing the extinctions. By playing a more prominent role in conservation biology, systematists could have made it clear that our discipline is of great importance in dealing with the human predicament and given us more of the opportunities I mentioned above. Here I want to examine why that hasn't happened and what changes we might adopt to make it happen.

WHY SYSTEMATICS HAS NOT BEEN A FRONT LINE DISCIPLINE AND WHAT TO DO ABOUT IT

One answer is clearly that systematists, like many colleagues in other disciplines, still adhere to the antique view that scientists should abjure participating in politics or "advocacy." I've discussed this silliness elsewhere (Ehrlich 2002) and won't belabor the topic here. I'll just remind you that when an epidemiologist says that SARS is a dangerous disease and recommends quarantine, she's not accused of being an advocate. But if a taxonomist asserts that the extermination of biodiversity could threaten the human future and recommends reducing human population growth and per capita consumption among the rich, that's often labeled advocacy. Some systematists have raised important issues in the face of the extinction crisis (e.g., Vane-Wright et al. 1991), but as a group we have not involved ourselves professionally in trying to solve the predicament to the extent that ecologists have — and the efforts of ecologists have hardly been adequate.

Another problem is that museums, where many taxonomists are based, are even more conservative than universities. A main (and valuable) contribution of systematics has been through its involvement in both supporting museums (for a particularly interesting summary, see Winker 2004) and botanic gardens and increasingly turning their exhibits toward informing the general public about the importance of preserving biodiversity. But only a few systematists have directly contributed to those latter programs. In the research area, Linnaeus would feel right at home in one of today's natural history museums as soon as he acquired a dictionary of cladistic jargon, as I pointed out in a much-too-optimistic article long ago (Ehrlich 1961b). Methods of preservation of most specimens would be much the same as in 1759 — stuffed bird and mammal skins, dried insects and plants, and so on. Too little effort has been made to start supplementary collections of specimens preserved in non-traditional ways, especially of model groups. We need more samples of, for instance, entire birds and butterflies (especially hatchlings of the former and eggs, larvae, and pupae of the latter) in fixatives. And more research should be pursued on the best ways of preserving internal organs for study now and in the distant future (Ehrlich 1964). On the positive side, though, there is an important trend toward providing long-term very deep freeze storage of many organisms to provide higher quality material for molecular systematists in the future.

The sampling of nature represented by traditional collections is still usually the exact opposite of "systematic" — emphasizing "good specimens" and adults. In the past it has sometimes been openly biased. I well remember N.D. Riley, keeper of the Lepidoptera collections at the British Museum (Natural History) (now the Natural History Museum, London), bragging to me in the

1960s that for a century the Museum had been buying collections, saving the “aberrations,” and discarding the “junk.” There are thus no population samples at the British Museum, for example, that would permit one to determine the frequency of melanic morphs of *Biston betularia* either before or after the industrialization of Britain. There are no proper samples in U.S. museums that would allow someone to see if a coevolutionary race between *Danaus plexippus* and its mimic *Limnitis archippus* can be documented, although both have been common butterflies. Curators do not yet see as their job assembling series of samples of selected “model” organisms to create opportunities to investigate microevolution and, perhaps, help to determine the more subtle impacts *Homo sapiens* may be having on the rest of biodiversity.

But I think the most important reason that systematics has had little impact on the preservation of biodiversity (and is ignored by most other biologists) is the narrow intellectual focus of the discipline. I believe there are many things we systematists could do to make our discipline more relevant and to increase its credibility with scientists and the public. One is to focus much more on the non-core aspects of our disciplinary mission — to employ that essential core as a launch pad for dealing with important theoretical questions in biology and crucial aspects of the human predicament. In the process of doing that and reallocating the efforts of systematists, I believe we will contribute much more to dealing with the sixth extinction. And it is my firm belief that systematists (and evolutionists and ecologists, as well as many other scientists) have an ethical obligation to put some substantial part of their professional effort into dealing with that extinction and other aspects of the human predicament.

The time is ripe for broadening and refocusing; where systematics is going is a pressing and relatively widely recognized question (e.g., Mallet and Willmott 2003). I suggest the following major changes:

1. Focus our theoretical thinking on the critical conservation issue of dealing with population diversity and on explicating the complexities of population differentiation.
2. Ask ourselves what kind of biodiversity database will scientists need fifty years from now, and what could and should systematists contribute to it? Then mount a major effort to create it.
3. Expand the frontiers of our discipline to encourage more collaboration with other scientists, from molecular biologists to linguists.
4. Overall, create a “21st century systematics” to replace the once forward looking “new systematics”, now well over six decades old (Huxley 1940). Insure that a major occupation of 21st century systematists is to help preserve biodiversity through targeted research and public education.

Other biologists can help encourage these changes both by learning more about the important ways in which systematics can expand our understanding of the world and giving moral support to those systematists who do “think big.”

I’ll now expand on these points.

FOCUS MORE ON POPULATIONS

One thing new systematists would do is cease the interminable armchair discussions of the definition and “nature” of species, and perpetually renaming them. The brilliant system developed by the Swedish botanist Carl Linnaeus (e.g., 1758) provides the foundation for biological nomenclature (Mayr et al. 1953). It has served science well for almost 250 years, but has not proven uniformly satisfactory (no taxonomic system could be) because of the many roles it must play. The system must communicate about multidimensional sets of morphological, behavioral, and genetic relationships, a process that always involves making arbitrary divisions in continua of evolutionary differentiation. The issue of the definition of species never concerned Linnaeus (who simply

took them for granted), but was given impetus by Darwin's choice of title for his classic work (Darwin 1859), and interested world-class biologists in the past (Dobzhansky 1937; Mayr 1942, 1957, 1963). It attracted much attention from philosophers (e.g., Ghiselin 1975; Hull 1976; Ruse 1987), mostly after it was no longer an appropriate focus for biological investigation, since the issue of "what is a species" was definitively recognized as insoluble (or, rather, badly posed) forty years ago. This is a point worth expanding, because one barrier to creating a 21st century systematics are the opportunity costs of smart-but-insular systematists beating this long dead horse.

The Species Problem

Research by my group on checkerspot butterflies played a role in demonstrating that the species "problem" was a non-problem, at least from the viewpoint of evolutionists and ecologists. First, a phenetic analysis of *Euphydryas editha* and *E. chalcedona* specimens (Ehrlich 1961a) showed that individuals assigned to two different species were related to each other in a variety of ways, showing different degrees of similarity. At that time it was also made clear that the genus *Euphydryas*, as well as a very large proportion of other Nearctic butterflies, did not divide neatly into distinct species (Ehrlich 1961a), a result that continuing investigations of *Euphydryas* assigned to the species *E. chalcedona*, *E. anicia*, and *E. colon* has abundantly confirmed (e.g., Brussard et al. 1989). Then, the discovery of the diversity of habitats, flight periods, oviposition plants, secondary host plants, nectar sources, population sizes, and population control factors among *E. editha* populations demonstrated that species comprised of genetically rather similar populations (Baughman, et al. 1990), were not necessarily ecological units (Ehrlich and Hanski 2004; Ehrlich, et al. 1975). And, finally, research on *E. editha* also showed that the genetic coherence of that species could not be credited to gene flow uniting population gene pools (Ehrlich and Raven 1969; Ehrlich and White 1980). The generality of this conclusion has not yet been established (Rieseberg 2001), so that the degree to which populations within a "species" in sexually reproducing organisms "evolve collectively" (Rieseberg and Burke 2001) should remain an important topic of research.

The basic reason that checkerspots (and the rest of the natural world) are not divided into easily-identifiable unambiguous units is, of course, that the dominant process of speciation creates continua of geographic differentiation. Such continua are displayed throughout Earth's biota in general (Ehrlich 1961a), and the checkerspots provide excellent examples. Phil DeVries, in his outstanding treatise on Costa Rican butterflies (1987:202), comments extensively on the difficulties of determining what should and should not be considered species in one group of checkerspots, the Phycioiditi (*Eresia*, *Anthanassa*, *Phyciodes*, etc.), and the problem with the Phycioiditi carries over into the Nearctic realm (e.g., Scott 1986:309-312).

Early phenetic results demonstrated the existence of continua of geographic differentiation; more recent research has shown that the same applies broadly to genetic differentiation as well. For instance, almost continuous degrees of genetic divergence are exhibited by checkerspot populations, regardless of which particular genes and populations are examined or method of analysis is employed (Baughman, et al. 1990; Brussard, et al. 1989; Brussard, et al. 1985; Wahlberg and Zimmermann 2000). Most evolutionists studying sexually reproducing organisms (especially animals) are satisfied to follow Ernst Mayr's (1942) lead and define as distinct species populations that are sympatric without showing abundant signs of hybridization, be they populations of lions and leopards, gold-crowned and white-crowned sparrows, or of *Euphydryas aurinia* and *E. maturna*. This sensibly recognizes the evolutionary importance of separate gene pools, even though technically determining the amount of interbreeding and hybridization can be complex (Ehrlich 1961a; Sokal and Crovello 1970). But when it comes to allopatric populations, the task of employing the

"potential interbreeding" criterion of the so-called "biological species concept" becomes impossible in all interesting cases (Ehrlich 1961a; Ehrlich and Holm 1962). Tests conducted in experimental sympatry can, of course, in some cases allow reasonable predictions of what actual interbreeding might occur in populations remigrated into sympatry in some at-the-moment undetermined selective environment in nature. Recently illuminated examples, such as the possibility that differentiated chimp and "human" lineages might have interbred for 3 million years after initial divergence (Navarro and Barton 2003; Rieseberg and Livingstone 2003) underline the problem of when and where to draw species boundaries under such criteria.

Plant biologists have not been over-concerned with species definitions in general, and the biological species concept in particular (e.g., Raven 1978, 1980a). Indeed, when asexual and fossil organisms are considered, it has long been obvious that what biologists call "species" are not all biologically equivalent entities. No narrow species definition will ever serve all purposes, and this is becoming widely recognized (e.g., Hull 1997). The definition used in any particular case depends on the question to be answered, and in some cases increasingly satisfactory solutions can be found (e.g., Sperling 2003). The best broad definition of species is simply "kind," for which might eventually be substituted some arbitrary level of phenetic or genetic divergence. Kind, in fact, has proven a quite useful definition in practice for both sexual and asexual organisms, because evolutionists, ecologists and behaviorists usually know what sort of entity is being discussed, and someone "twitching" birds or butterflies on a life list ordinarily doesn't care. The same can be said for cryptic kinds that can only be separated by biochemical techniques, a phenomenon that is likely to be very widespread (for a recent example, see John Burns' and Dan Janzen's work described in Pennisi 2003).

Despite all this, as late as 1998 one taxonomist was able to write " 'What is a species?' is considered one of the central issues of biology as well as one of its most vexing problems" (de Queiroz 1998:72). Another taxonomist expressed the view that the "nature of speciation processes can only be investigated and understood when there is agreement on the nature of species" (Claridge 1995:38). In fact, the vast majority of biologists pay not the slightest attention to the "problem" of "What is a species?" One might better stand Claridge's argument on its head and say that we'll understand much more about the variety of entities we conveniently call species when we more thoroughly understand the processes of population differentiation. Substantial progress has been made in elucidating that differentiation by scientists who are not deterred because species are named for convenience in communication and are not all presumed to be the same kinds of entities (e.g., Bush 1994; Coyne 1992; Ehrlich and Raven 1969; Grant and Grant 1997; Kaufman, et al. 1997; Orr 2001; Orr and Smith 1998; Rieseberg 2001; Schwarzbach and Rieseberg 2002; Turelli, et al. 2001; Via 2001; Wu 2001). What would we think if Earth scientists were perpetually wondering "What is a mountain?" and writing papers talking about "good mountains" and "bad mountains" and analyzing different "mountain concepts" instead of focusing, as they have, on different forces in orogeny and erosion? What if they stated that the nature of processes responsible for topographic relief can only be investigated and understood when there is agreement on the "nature of mountains"? For a tiny sample of the more recent literature on the species non-problem, see Mischler and Donoghue (1982); Cracraft (1983); Patterson (1985); de Queiroz and Donoghue (1988); Nixon and Wheeler (1990); Vrana and Wheeler (1992); Vogler and DeSalle (1994) Mallet (1995); Davis (1996); Avise and Wollenberg (1997); Claridge et al. (1997); Mayden 1997; Harrison (1998); Sterelny and Griffiths (1999); and Hey (2001).

Nothing I have said here should be interpreted as demeaning the fundamental importance of investigating the processes of population differentiation. Among other things, understanding them will help us better evaluate the sorts of processes that need to be protected in order to permit the

continued generation of diversity — something that could be vital to restoration biology. In any case, it is clear that we still suffer from a lack of information on population differentiation in nature, where the few detailed studies that have been done (e.g., Ehrlich and Hanski 2004) suggest that species are much less unitary entities than museum and laboratory research suggests. It may be a hopeless suggestion, but I would prefer that the phrase “population differentiation” increasingly substitute for “speciation.” It would get away from the psychological need, which seems to persist, to define species as all the same sorts of units, such as “the most inclusive entities that directly participate in evolutionary processes” (Rieseberg and Burke 2001).

The dominant species-centric biodiversity paradigm (e.g., Claridge et al. 1997) has unfortunately resulted in an emphasis in conservation biology on the preservation of species, and thus helped perpetuate the neglect of the equally important (in many cases more important) issue of the preservation of populations (Ehrlich and Daily 1993; Hughes et al. 1997; Hughes et al. 1998) and, thus, ecosystem services (Daily 1997). That has been a distinctly negative (if inadvertent) impact of systematics on the conservation of biodiversity.

Subspecies and the Systematics of Populations

A question long debated by taxonomists and of interest to conservation biologists is whether or not to recognize taxonomic entities below the level of species. That subspecies are not ordinarily evolutionary units (because of discordant character variation) was pointed out 50 years ago by Wilson and Brown (1953), and studies of butterflies (e.g., Gillham 1965), including some by our group on checkerspots (e.g., Baughman et al. 1990; Brussard et al. 1989), have supported this view. There is, of course, considerable interest in studying patterns of genetic variation within species (Avice 1994), and in some circumstances subspecies names can make biogeographic and phylogeographic discussions smoother. But there is usually only one reason to name and describe new subspecies today — and it is connected with the human predicament. In some circumstances, populations in danger of extinction can be protected legally if they are designated as subspecies. That utility would disappear if more sensible laws aimed at preserving humanity’s natural capital were put on the books. Unhappily, rather than just making that designation when it appears worth the effort, taxonomists have been pushed into a biologically empty debate about what is an “evolutionarily significant unit” within a species (Moritz 1994; Ryder 1986) by the needs of policy makers to come up with rules for what entities to protect. As Tom Brooks cogently put it, at the global scale this amounts to “fiddling while Rome burns” (quoted in DeWeerd 2002) — but some fiddling may actually help quench a few local blazes.

It is a major challenge for 21st century systematics to find scientifically sound new ways of dealing with the systematics of suites of populations, in the process providing a more rigorous basis for monitoring (and countering) the ongoing decay of population diversity. For too long the magnitude of biodiversity loss has been measured by the rate of species extinctions, an approach that understates the seriousness of the problem and masks some of its most important consequences. A 21st century systematics of populations would take into consideration changes in their numbers, dynamics, distributions, and genetic compositions, as well as the consequences of such changes for ecosystem functioning and the delivery of ecosystem services (e.g., Luck et al., in press). And at the population level, as at the species level, a modern systematics would necessarily sample nature, not attempt to be comprehensive. Even large-scale application of ever-more-automated molecular fingerprinting techniques will not allow monitoring of more than a tiny fraction of the billions of natural populations. When one considers how much is already known about population and metapopulation structures in checkerspot butterflies (Ehrlich and Hanski 2004), and how much

more there is to discover, it becomes crystal clear that population systematics can be developed for only a tiny and carefully selected subset of populations.

BUILDING THE BIODIVERSITY DATABASE

It is high time that systematists organize themselves to create a database that will be useful throughout biology. It will be a very large task, but it will focus the efforts of the discipline and place it in its rightful position within biology — the most important sciences of the 21st century. But in the process systematists should keep in mind three very important tasks.

Do more to stabilize nomenclature. We can't build a successful biodiversity database without greatly reducing the near constant changing of names of taxa that infests systematics. The names we use must be understandable not only to systematists, but to the other scientists who will be major users of the database and to the general public. My recent experience with a many-authored book on checkerspot butterflies (Ehrlich and Hanski 2004) demonstrates the basic utility of the Linnaean nomenclature system for communication among scientists. Fifteen co-authors had no difficulty letting each other know exactly which organisms were being discussed, and were perfectly relaxed about the ambiguities that are inevitable when imposing a discontinuous system of names on a natural system that is permeated with various continua. And our colleagues who work on other systems should easily understand to which organisms, checkerspot, host plant, or whatever, we are referring. The same can be said for the communication among specialists about butterflies in general in symposia and in the production of a recent book on the entire butterfly model system, spearheaded by Carol Boggs (Boggs et al. 2003).

Indeed, if those interested in biology had stuck to the Linnaean system (originally designed for international communication), treated the expanded Linnaean hierarchy conservatively (Ehrlich and Murphy 1981), and changed names only *in extremis*, our job would have been even easier. The multiplicity of "scientific" and artificially generated "common" names (Murphy and Ehrlich 1983), and the instability of both, is a central reason that systematics is an unappreciated discipline. Most scientists and nature lovers are only exposed to it in the form of very frequent, very annoying, and often senseless, changing of names. Worse yet, the discipline is now debating changing all names, including all species names, to ones based on the uncertain and (for communication) relatively uninformative estimates of recency of common ancestry (Donoghue 2001; Pennisi 2001). Most people, including most biologists, are not much interested in relationships based on relative times of divergence. They care little when the lines leading to birds, crocodiles, and lizards split from one another — they are much more concerned with communicating about the phenetic relationships of those organisms, the phylogenetic relationships that are based on time and rate of evolution. Told that a "Birdcroc" is sneaking up on her, a naturalist wouldn't know whether it would sing her a song or drag her into the lake and eat her. This means (horror of horrors) that for communication with non-systematists, I'm in favor of retaining paraphyletic taxa.

This is a topic on which reasonable people can differ, of course. One can argue that, if a well substantiated branching tree of life can be created, that a more stable nomenclature could be based on it, with the standard of monophyly adopted throughout. This would ignore the rate aspect of evolution, but its basis would be clear. But would such a system be practical to create? It is one thing to estimate branch-time trees for a sample of biodiversity, and then compare them to phenetic trees to get some idea, for instance, of how frequently there are very rapid radiations. It would be quite another to try to work out branch times for all taxa, even just going up to the genus level. I don't think it would be worth the effort. But it would be worth the effort to develop and use some sort of coding system for at least base taxa (individuals, populations, species) for the biodiversity

database. These could supplement the use of the Linnaean system and be used by the database's gatekeepers to route incoming data properly.

In any case, as long as the Linnean system is the main one in use, every effort should be made to avoid changes in the latinized names of obligatory categories, and journals should refuse to publish any name changes that do not reflect stunning new results (i.e., at the level of finding out that two "species" are actually males and females of the same population). Changing the status of allopatric populations wouldn't ordinarily qualify, nor would deciding a genus was only a subgenus or vice-versa. Only a handful of people care at all whether *Euphydryas anicia* is a "good species" or a "subspecies" of *Euphydryas chalcedona*, and the question is close to meaningless in any case.

So what to do? Some steps could be relatively simple. Coining of more common names should cease; *Euphydryas* or *Castilleja* is no more difficult for a layperson to learn than hippopotamus or chrysanthemum. Once a system of database codes are agreed upon, stabilization committees should be established for all major (especially model) groups, whose first charge will be to approve the names of all lower taxa within that group and match them to the biodiversity database codes. That would both help to avoid name-changing that would confuse non-systematist contributors to, and users of, the database, and would minimize the inevitable mis-assignment of data. Remember that the vast majority of specific names are never used in a context where using a different name would make the slightest practical difference. Indeed, it would be interesting to see if the majority of specific names are ever used beyond the original description and subsequent catalogues and taxonomic re-shufflings. Above all, systematics should reduce its focus on names (or bar codes, or whatever) that we use as "convenient landmarks in the continuum of life" (Ehrlich 1961b) and concentrate more on keeping that continuum going and elucidating the kinds and mechanisms of its differentiation.

Recognize that "completely" describing the tree of life is impossible. Some believe that the task of systematists "is to chart the diversity of life, in its entirety, from the tiniest tips of the tree to every one of its branches" (Donoghue 2001:755). Of course, technically the tiniest tips (twigs) of the tree are all individual organisms, recent and past, that are post-reproductive or died without leaving offspring (I am a twig!). But knowing the context, we can assume that the statement refers to species (however defined) as "tips," and "to chart" includes writing superficial species descriptions and arriving at some sort of estimate of times of occurrence of the myriad fuzzy crotches of the phylogenetic tree. Even completing the job using species as the tips would still be quite an ambitious, and in my view scientifically questionable, project. Species are often not unitary "tips" — ecological or genetic units — but rather complexes of interrelated entities in constant flux as environments change. Demographic units go extinct and are reestablished, and populations evolve in response to varying selection and migration pressures and genetic drift (Ehrlich and Hanski 2004). To paraphrase Heraclitus, "you can't collect the same species twice."

Systematists should be more evolutionary. Describing the nature of the twigs of the tree today at the population level (e.g., population and metapopulation demographic and genetic structure), has barely begun, even for model systems. And definition (and temporal estimation) of the crotches is fraught with problems. Long ago, simple analysis showed how futile a goal was the "complete" charting of continuously evolving life — even before its complexity was understood as it is today (Ehrlich 1961b, 1964). In the light of the accelerating extinction crisis, that goal now looks particularly ludicrous, and the opportunity costs of trying to achieve it substantial. Furthermore, that description, if miraculously achieved, would be instantly obsolete and unlikely to do much help solve the human predicament.

Start sampling nature in order to understand its diversity better. Because of the lack of well-designed, taxonomically and geographically stratified sampling, many major systematic questions

are not much closer to solution today than they were in 1950. Fortunately, there is movement in the direction of judicious geographic sampling, as exemplified at the California Academy of Sciences, with its emphases on expeditions to key places such as Madagascar, the islands of the Gulf of Guinea, and Yunnan in China.

It is now much too late to expand our knowledge of biodiversity much by continued random additions to the existing crude systematic/genetic/ecological/behavioral overview of the vast panoply of biological diversity. A major, well-funded effort could help (Raven and Wilson 1992), but that effort does not seem to be feasible politically because it has no obvious scientifically or practically useful goal. Still, as I have emphasized elsewhere (Ehrlich 1997:23–33; Ehrlich 2001), it is not too late to develop a substantially more detailed and useful understanding of a limited number of model groups — comprehensive pictures of their diversity, distribution, and ecological relationships (see also Raven 1980b). We know little about the degree to which species in most groups are or are not ecological units or genetic units (bound together by gene flow). The investigation of population and metapopulation diversity has barely begun. Systematists have only a rough idea of the relative diversities of major taxa in various communities. The issue of dissonant phenetic evolution of life-history stages has barely been explored.

Deep knowledge of sample groups could begin to answer questions in those areas. It could also help in plotting strategies for conserving biodiversity and honing human judgments on key questions such as taxonomic substitutability (redundancy) in ecosystem services, central issues in solving the human predicament. It could make estimation of extinction rates more precise. It could also help highlight a less-appreciated aspect of the human predicament — the enormous loss of Earth's heritage of information as expansion of human activities deletes much of the “experience” stored in DNA as a result of eons of evolution (loss of the diversity of human languages is an analogous tragedy now well under way). Thorough understanding of some model groups could provide a framework of understanding for population biologists in a century or so when much of today's biodiversity will exist only as museum specimens or fossils. Think of how much better we would understand processes of the diversification of life and our own origins if we had comprehensive studies, done at the time, of Cretaceous dinosaurs, birds, and plants — or of the primates of eight million years ago (when the common ancestors of chimps and people were alive)!

A database to assemble comprehensive information on a well-stratified sample of taxa could make a big contribution toward generating answers to many important questions in biology in general and conservation biology in particular (Ehrlich 1997; Sisk et al. 1994). One step in that direction is represented by the NSF's “Tree of Life” program (www.nsf.gov/pubs/2004/nsf04526/nsf04526.htm; <http://tolweb.org/tree/phylogeny.html>), which focuses on the “phylogenetic resolution of large lineages or clades,” but imagines it will eventually deal usefully with 1.7 million species. Describing the relatively permanent basic architecture of a tree is feasible and reasonable (for a recent fine example, see Feild 2003); describing it down to its tiniest, ever-changing twigs is neither. With the *Tree of Life*, and related efforts like that of Brent Mishler and his colleagues (Mishler et al. 2003), to create phylogenetically structured databases, a framework for organizing our samples of biodiversity may already be emerging. Building on that framework to produce a useful tree of life would be an ideal megaproject for 21st century systematics. It would need to be much more focused than an attempt at creating a complete list of species and an indication of their putative cladistic relationships. The megaproject could broaden systematics by establishing many contact points with the geneticists, ecologists, developmental biologists, neurobiologists, behaviorists, climatologists, GIS specialists, soil scientists, hydrologists, oceanographers, and other researchers. The other scientists could both contribute data and work with the database. Computer scientists, in turn, could aid in making the database the state-of-the art standard.

The database should be designed for problem solving, and its creation would be a cooperative venture whose appeal would in part be its demonstration of the tight interdisciplinary connections that more and more are features of modern science. It would put systematics at the center of things rather than the periphery. Two questions posed to me recently could be almost instantly solved if such a database existed with butterflies, ants, birds, and mammals included as well-developed sample groups, and appropriate geographic and morphological data were included. They were: (1) how frequently is topographic heterogeneity a key to persistence of populations of small-bodied animals? and (2) is the forward position of the clitoris in bonobos and people an adaptation to facilitate female-female bonding? All of you can think of many other interesting questions, and other sorts of data that, if included in the database, would be helpful in answering them.

The criteria for selection of model systems to build into the database should be under continuous discussion, but would include sampling of ecological, geographic, and systematic diversity, direct importance or interest to human beings (including through the delivery of ecosystem services), and potential for "completion." Groups that might be chosen under the potential-for-completion criterion today include most vertebrates, vascular plants, and, my own favorite group, butterflies. The Papilionoidea are the most obvious taxon of the invertebrates to select as a model group for accelerated systematic, ecological (including ecophysiological), evolutionary, and behavioral study. Butterfly researchers already recognize this (Boggs, et al. 2003; Ehrlich and Hanski 2004; Watt et al. 2003), and it is to be hoped that many more systematists can be recruited to their ranks. Butterflies also can serve as a wedge to break the tendency of conservation groups and governments to concentrate their attention on vertebrates — an egregious error in a world where preservation of ecosystem services must be a conservation priority.

Birds, butterflies, and mammals deserve more attention because amateurs can easily be co-opted into efforts to comprehensively understand them, and because of their symbolic and ecotouristic importance (but see, Sekercioglu 2002). Other relatively well-understood arthropod groups that might serve as models include ants (Beattie 1985; Gordon 1999; Hölldobler and Wilson 1990), because of their incredible importance in ecosystem functioning, especially in the tropics; bees because of their key roles in pollination (Michener 1974, 2000); mosquitoes, ticks, and other organisms of public health importance, and tiger beetles, which have many attributes that would make them good indicators of biodiversity (Pearson and Cassola 1992) and would serve, as predacious insects, to provide a nice comparison to the butterflies. In terms of the human predicament, attention to organisms that are vectors or reservoirs of pathogens, and to the pathogens themselves is especially important in view of the deteriorating epidemiological environment (Daily and Ehrlich 1996a).

Focusing attention on understanding already well-studied groups has several enormous advantages. First, in some sense it is possible that we'll be able to "complete" them — providing comprehensive pictures of the evolution of at least a sample of branches on the tree of life. Efforts to "complete" the taxonomy of vascular plants are well under way, centered in institutions like the Missouri Botanical Garden, the Royal Botanic Gardens, Kew, and the New York Botanical Garden, and important issues in the origin and evolution of the flowering plants are gradually being elucidated (Ackerly et al. 2000; Friedman and Floyd 2001). Every time a new detailed study of the systematics of a butterfly group appears (e.g., Penz 1999; Penz and DeVries 2003), we inch further out on the asymptote of understanding a classic model taxon (Boggs et al. 2003). Even among vertebrates, great opportunities obviously remain for expanding knowledge of their diversity and patterns of radiation (e.g., Mayr and Diamond 2001; Meegaskumbura, et al. 2002), and some of the work on phylogenetics of large vertebrates may eventually prove useful in interpreting the human past (e.g., Hassanin and Douzery 2003).

All of this does not mean that I think all revisionary and exploratory work should be done on model systems. Whenever I look at a sample of gorgeous and diverse tropical Hemiptera or Hymenoptera, or even subalpine flies (Hughes, et al. 2000), my taxonomizing instincts rise to the surface and my mind is flooded with phylogenetic questions. Surely all of us should spend some time exploring, asking questions, doing research, and enjoying organisms that are not necessarily suited for use as model systems (but may have overlooked potential in that area). And data from such exploring could be integrated into the database. But in my view that does not free us of an obligation to our discipline and to humanity to put some substantial portion of our effort into more deeply understanding those important samples of biodiversity.

EXPAND THE BOUNDARIES OF OUR DISCIPLINE

There are steps beyond creation of a comprehensive biodiversity database that would help to expand the usefulness, recognition, and support of systematics. One would be to expand collaborations with molecular biologists and make sensible use of genomic information. Techniques developed for systematics have certainly been essential to biologists with an interest in molecular evolution (e.g., Felsenstein 1985; Harvey et al. 1996), and molecular data have been central to efforts of systematists to sort out the patterns of phylogenetic branching, most famously in the recent branches of our own family tree (e.g., King and Wilson 1975; Krings et al. 1997). But two related erroneous ideas now combine increasingly to constrain and marginalize systematics. One, of course, is that temporal relationships based on splitting time are the only important aspects of phylogeny (see discussion in Ehrlich 1997:23ff). The other is that information on nucleotide sequences is somehow more important or fundamental than information on any other aspect of the phenome (Ehrlich 1964) (the genotype is the information coded into the nucleotide sequence, but the sequence itself is part of the phenotype). The additional systematic information provided by DNA should not be used as the primary basis of general taxonomic classifications (Tautz et al. 2003), as Christopher Dunn points out (2003). But its value to taxonomy and in systematics related to conservation (e.g., Baker et al. 2003; Baker et al. 2000; Baker and Palumbi 1994, 1996; Palumbi and Cipriano 1998) can hardly be overestimated.

How sequence information should be employed depends on the kinds of questions being asked. Phenetic relationships are often more useful to understand than branching times (as in the bird-crocodile case) — phylogeny does, I repeat, have both rate and time dimensions (see also Lipscomb et al. 2003; Seberg et al. 2003). In the case of nucleotide sequences, information on aspects of the phenome other than those sequences may be much more instructive. For instance, the small sequence differences between chimps and people so far have been of little interest to scientists (except for surprise at the paucity of differences and a growing fascination with the developmental issues thus raised) as compared to the morphological and (especially) behavioral differences and similarities of the two organisms. On the other hand, recent work showing that the skipper butterfly, *Astraptes fulgorator*, is actually a complex of perhaps ten or more sibling species (Pennisi 2003; Stroh 2003) casts new light on a significant puzzle in plant-herbivore coevolution. If systematics is to thrive, it must place the important topics of branching times and sequencing into the perspective of a broader 21st century systematics and focus on them primarily when they can be used to answer important questions.

Furthermore, molecular systematics is opening the equivalent of a vast new area to taxonomic, evolutionary, and ecological exploration. Collaboration with microbial ecologists and evolutionists in examining the taxonomic structure of the worlds of Archaea and Bacteria (rather than the two specialized offshoots of the Eucarya where most of us have concentrated our efforts) seems

sure to yield fundamental insights into the structure and evolution of the main body of biodiversity (e.g., Pace 1997). It's as if there were a whole new planet of organisms barely explored, in a pre-Linnaean state, about which one might develop novel taxonomic ideas. If systematists don't get more involved in this exciting enterprise, then they will be left behind here too as others proceed to ask the critical questions (Bohannan and Hughes 2003; Horner-Devine et al. 2004; Horner-Devine et al. 2003).

Systematists should also start more research on problems of broad interest to other biologists and other scientists. A 21st century systematics would have the potential of capturing much more relevance and interest if it expands its disciplinary boundaries far beyond routine description and the hypothesizing of branching-time relationships that preoccupy so much of the discipline today. Systematics has had too much of a tendency to be a stand-alone science. Just as world-class ecology is now interfacing with atmospheric chemistry, climatology, economics, and environmental engineering (to name a few), a 21st century systematics would feature many more collaborations with ecologists, evolutionary geneticists, conservation biologists, developmental biologists, neurophysiologists, linguists, cultural anthropologists, philosophers (especially in this age of deconstruction), and so on.

Much more of the focus of 21st century systematics, as indicated in the database discussion, could be on contributing systematic (both phenetic and branching-time) insights into the evolutionary structure of carefully selected model groups, and collaborating more closely with the molecular geneticists now attempting to look in detail at patterns of population differentiation. As other examples, the new systematists could do comprehensive censuses of a stratified sample of "May plots" in order to get an comprehensive view of the ratios of species diversities of various taxa (e.g., May 1988), and to examine carefully the systematic assumptions built into such ratios (i.e., how species and higher taxa in the surveys are to be defined). Twenty-first century systematists could promote and control the global terrestrial monitoring system I proposed earlier (Ehrlich 1997:80–83); that would be "big science" with a critical importance.

Systematists could reexamine many issues related to measures of community diversity by including the phenetic dimension of diversity (e.g., Hendrickson and Ehrlich 1971). After all, in the metrics normally used by ecologists, a lizard community consisting of six *Anolis* species is fully as diverse as one containing one *Eumeces* species, one *Cnemidophorus*, one *Phrynosoma*, one *Sceloporus*, one *Heloderma*, and one *Anolis*. Systematists could also put more effort into examining the degree to which morphospecies can reasonably be used to assess conservation situations where conventional taxonomic treatments are not accessible; indeed, much of the pioneering systematic work on monitoring has been done by non-systematists (Beattie and Oliver 1994; Daily and Ehrlich 1996b; Oliver and Beattie 1993, 1996a, 1996b). And they could extend the standard taxonomic process of mapping species distributions (think of all those maps with black dots) to use new techniques to predict distributions as functions of the abiotic environment (e.g., Fleishman et al. 2003) or more complete habitat information. The latter is being pursued at a very high level at CONABIO, the Mexican biodiversity institute. Among other things, the Mexican scientists are using the new techniques to predict rates of invasion of *Cactoblastis cactorum*, which threatens to be a serious agricultural pest in Mexico, and of Chagas disease, a potentially nasty public health problem. The techniques are also being used to judge where release of certain genetically-modified crop strains are permissible, and to determine locations of possible suitable habitat patches for the endangered swallowtail butterfly, *Baronia brevicornis*, (Jorge Soberon and José Sarukhan pers. commun.).

The 21st century systematists could have as a major goal developing new model systems to explore novel and interesting ecological questions. An important current example is the work of

John Thompson and his collaborators on selection mosaics and coevolutionary hotspots (e.g., Thompson 1994; Thompson and Cunningham 2002). Their work, and that of others (e.g., Benkman et al. 2001; Hochberg and van Baalen 1998; Zangerl and Berenbaum 2003) has been demonstrating that in addition to species not being ecological units, their coevolutionary interactions also often vary from population to population. For instance, Benkman and his colleagues (2001) have shown, largely by analyses of geographic variation in crossbill bills and conifer cones, that the coevolutionary interactions of crossbills and conifers vary from population to population, at least partially in response to the presence or absence of the red squirrel (*Tamasciurus hudsonicus*), a crossbill competitor. The consequences for the human epidemiological environment of potential population-level differences in pathogen-*Homo* or pathogen-reservoir coevolution have barely begun to be explored and would be a highly relevant field for investigation by 21st century systematists. So would targeted studies of such crucial complexes as hantaviruses and their muroid hosts (Yates et al. 2002).

One substantial opportunity for new systematists to find funding for relevant research would be through the National Ecological Observatory Network (NEON) being promoted by the National Science Foundation (<www.nsf.gov/bio/bio_bdg04/neon04.htm>). At the moment the projected role in it for the systematics community shows no grasp of how one should actually approach an important scientific problem — in this case how best to monitor changes in biodiversity, determine their causes, and project the magnitude and directions of future changes. (<ibrcs.aibs.org/reports/pdf/NEON5_June2002.pdf>). Twenty-first century systematics should be at the forefront of developing the most cost effective (as opposed to instrument-intensive) ways of accomplishing this.

Finally new systematists should expand the search for other disciplines in which systematic techniques can be applied. One obvious area to be mined is in cultural microevolution (Ehrlich 2000:228–229). We need to know much more about how languages, religions, norms (e.g., attitudes toward aggression and civil rights), and so on evolve. It is an area where the approaches and ideas of systematists could have great impact — if we remove our disciplinary blinders and give it a try. One important way to get rid of those blinders, and one where other biologists can help, is to start holding more joint meetings of systematists with ecologists, evolutionists, conservation biologists, social scientists, and others. That would promote interdisciplinary thinking, enrich two or more disciplines at once, and (if properly structured) lead to a broadening of graduate training in systematics — which may be the most critical of all needs in reforming the discipline. One can imagine the shrinkage that would occur in the “what is a species” literature if every systematist, as part of his or her graduate work, were required to do an appropriate field project on population differentiation in a model group.

CREATING A 21ST CENTURY SYSTEMATICS SHOULD BE FUN

In closing, let me note that continuing to name and estimate phylogenetic branching times for random parts of organic diversity is at least as reasonable a thing to do as was (is) describing and naming geographic features of Earth or stars in the heavens, or cataloguing a rich and unique library. It would be great to have the capability of somehow storing and making accessible life's entire DNA library and the information stored as myriad phenotypes. Naming and cataloguing is also fun, and we all should have some fun in doing our science. If working out branching times for a group of Amazonian mites or New Guinea midges is your thing, then by all means — enjoy! But put at least some of your time into research that will be more likely to aid directly in solving the human predicament. As I hope I've indicated, there are plenty of such activities for 21st century

systematists, where important questions can be asked, important hypotheses tested, and, above all, results pertinent to the preservation of biodiversity obtained. That preservation is the most critical and difficult goal of 21st century systematics — if we don't succeed, there soon will be no basis for answering any crucial scientific questions systematists have not yet recognized. Saving biodiversity and dreaming up and answering those questions are our job; they will allow future generations of systematists (and other people) to enjoy Earth's living heritage and have more fun. So let's get on with it.

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How Much Biodiversity for the Future: Our Choice, Our Responsibility

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The papers in this symposium volume illustrate many effective approaches to carrying out an inventory of the world's organisms. Some advocate a survey as complete as possible, others a sampling approach. All would like to see as extensive a series of studies on the biodiversity of the Earth as we can manage. Some groups of organisms, such as nematodes, fungi, and mites, are so poorly known that it does not seem possible to inventory them completely within any reasonable period of time. For the prokaryotes, bacteria, and Archaea, completing an inventory is so difficult that no clear picture of their diversity has emerged yet, despite their enormous importance for us.

Because it is so daunting to attain a comprehensive picture of Earth's biodiversity in an age of extinction, I consider that it would be best to develop relatively complete inventories of those groups that are relatively well known, such as vertebrate animals, plants, butterflies, and a few others. For more incompletely known groups of organisms, it seems to me that it would be more constructive to devise rational methods of sampling than to continue our present approaches as if a complete inventory will be possible. With appropriate sampling, we could estimate the dimensions of global diversity and outline biogeographical patterns. At the same time, it seems important to study the whole constellation of organisms that occur in particular places that are important because of the broad ecological and other studies that are conducted there. Such places certainly include La Selva in Costa Rica, Barro Colorado Island in Panama, and Hubbard Brook in Connecticut — places where it would be of great interest to understand the interactions of all kinds of organisms. In general, Long Term Ecological Research (LTER) sites, established by the National Science Foundation in the 1980s and emulated throughout the world, in many cases have been surveyed for biodiversity and would serve such purposes well if studied over the years in even more depth. This is basically the strategy laid out by Raven (1980).

EXTINCTIONS PAST AND PRESENT: HOW MANY SPECIES ARE WE TALKING ABOUT

Our current level of knowledge of eukaryotic organisms on Earth is very poor, with some 1.6 million named of a total that very probably exceeds 10 million; only a few thousand of these are known to a reasonable degree of detail (May 2000). For prokaryotes, as mentioned, we have no real idea of how many there may be, and any estimates are premature (Dykhuisen 1998; Curtis, et al. 2002). There are relatively few systematic biologists fully employed in developing an inventory of any group of organisms, and far more species exist than they could possibly catalog within a reasonable period of time. Despite our collective lack of knowledge, we expect to be able to utilize organisms, many of them unknown at present, in a variety of ways that would contribute to the sustainable production of food, medicine, shelter, and clothing — and yet we have not even recorded the existence of at least five-sixths of them, and perhaps an even higher proportion!

We also would like to understand the ways in which organisms occur together in communities

and ecosystems, and to enhance the ecosystem services that they provide in such abundance and without any direct cost to us. In an age of molecular biology, comparative genomics, and the possibility of gene transfer between distantly related species, our global stock of organisms has taken on a new meaning in relation to our efforts for building sustainability for the future. If the present century is to be "the age of biology," we need as many kinds of organisms as we can save to build that age. We enjoy and appreciate organisms, and wonder about their effects on the nature of our origins, our language, our psychologies, our brains. Obviously, we are completely connected with them in an extraordinary range of ways.

We also worry very much about the rate at which our population growth, increasing levels of consumption, and use of inappropriate or unsustainable technologies are driving them to extinction. Some 65 million years ago a giant asteroid collided with the Earth at a position that is now off the end of the Yucatán Peninsula in Mexico, throwing up a long-lasting, dark cloud of debris that ultimately brought about the extinction of an estimated two-thirds of all terrestrial species (Pimm and Brooks 2000). Following millions of years of recovery from that catastrophe, the number of eukaryotic organisms began to climb towards the estimated 10 million species that exist now.

Over the long period of time that followed the asteroid collision, some 65 million years, we judge rates of extinction from the fossil record of groups of organisms that have hard body parts, and which are, therefore, well preserved in the fossil record. From such examination, it can be estimated that the average life of a species has been several million years (Pimm 2001). On average, about one species per million has gone extinct per year. Over the long period since the last major extinction, 65 million years, those species that have disappeared have been more than replaced by newly-evolved ones as the total number has climbed toward its present level. The pace of extinction has, however, increased markedly during the past few centuries, as I shall discuss in more detail. General reviews of the topics treated in the next few paragraphs have been provided by Pimm (2001) and Raven (2001, 2002), among many others.

Following the development of crop agriculture some 10,500 years ago in the eastern Mediterranean region, a rapid human population explosion took hold. Villages grew into towns and ultimately cities, while the fabric of civilization became increasingly complex. Within the past 2000 years, the number of people on Earth reached several hundred million, then 1 billion for the first time in the first half of the 19th century, 2 billion in 1930, 2.5 billion in 1950, and 6.3 billion in 2003, according to figures supplied by the Population Reference Bureau. These increases in population were accompanied by increases in the level of consumption per person, and those increases have been very unequally distributed as societies have become stratified. More recently the stratification has been intensified with the development of political units, which in our day are basically nations.

As we enter the 21st century, about 20 percent of the people on Earth, those who live in industrialized countries, control about 80 percent of the world's wealth. In general, they consume at a level 30 to 40 times that of rural people in developing countries. Overall, our collective level of consumption has been estimated by Mathis Wackernagel to amount to 120 percent of what the planet can produce sustainably, having increased sharply from 70 percent in 1970, and still continuing its precipitous climb upward (Wackernagel, et al. 2002). All over the world, people are planning to consume even more in the future, as many developing world economies, notably those of China and India, grow very rapidly.

Although some of us live very rich lives, with levels of consumption that would have been unimaginable just a few decades ago, most human beings live lives of abject poverty — half of all the world's people subsist on less than \$2 per day, and a quarter of us on less than \$1 per day. Approximately half of the people on Earth are malnourished in respect to some essential dietary

requirement, and a sixth of our total population consists of people who are literally starving — surviving on less than 80 percent of the U.N.-recommended minimum caloric input per day, so that their bodies are literally wasting away and their brains fail to develop properly when they are children. As we have seen, the human population is already consuming the world's resources at 120 percent of the rate at which they are being replaced. Our total population, by moderate estimates, is projected to grow by an additional 2 billion people before it starts to stabilize around the middle of this century. In the face of these numbers, it does not appear structurally possible to improve the lot of most people without seriously rethinking what each of us needs, how it is going to be obtained, and how we can improve our relationships with and understanding of one another.

To mention a few specific environmental effects, the combination of population growth, affluence (consumption), and non-sustainable technology is having a very obvious negative effect on the global environment. Since 1950, an estimated 20 percent of the topsoil, 20 percent of the agricultural land, and a third of the world's forests has been lost, while the CO₂ in the atmosphere has increased by about a sixth and the stratospheric ozone layer has been depleted 6 to 7 percent. In the early 21st century, we are estimated to be using, wasting, or diverting at least 45 percent of the world's terrestrial photosynthetic productivity and 55 percent of the world's sustainable supplies of fresh water (Vitousek, et al. 1986; review in Pimm 2001). No wonder that the rate of extinction of biodiversity is increasing rapidly!

How can we determine this rate if we have named only about a sixth of the estimated number of species of eukaryotic organisms? It can be approximated by referring to what is recorded about the members of well-known groups — largely vertebrate animals and vascular plants, together with a few others such as butterflies, some groups of beetles and mollusks, and so forth. Using the estimate presented earlier of one species per million per year over the past 65 million years as a baseline, we can examine subfossil records and publications over the past 300 or so years, since the time when people began to describe the living world adequately, and by doing so estimate what the extinction rate has been during this period (Pimm and Brooks 2000). For the relatively well-known groups of organisms just enumerated, we can estimate that the extinction rate has climbed to hundreds, and now thousands, of species per year. Where is it going?

In making this determination, it is important to examine the effects of the four prime causes driving the process of species extinction in the 21st century. The first and most obvious of these is habitat destruction. The relationships demonstrated in the field of island biogeography have shown that the relationship between species number and area either for islands or on the mainland in a more or less uniform habitat is a logarithmic one. Thus the reduction of an area to one-tenth of its original size will lead to the extinction of approximately half of the species that occurred there originally. The tropical moist forests remaining by mid-century are projected to constitute about 5 percent of their original area, and inasmuch as these forests are estimated to be home for about half of the species on Earth (perhaps five million species or more), such a reduction could in itself lead to the loss of about a third of the estimated number of eukaryotic species (Pimm and Brooks 2000). In a major chapter of recent extinction, the loss of habitat as the Polynesians colonized the islands of the Pacific over the past 1500 years and cleared their lowlands and valleys for agriculture, combined with their hunting activities, is estimated to have led to the loss of as many as 1000 species of birds there, of a world total of some 9000 species, over this short period of time (Pimm 2001).

Hunting and gathering wild species of plants and animals are another important cause of extinction focused on a particular species. For example, hunting bush meat, an activity that is particularly important in Africa, coupled with increasing numbers of people, is seriously damaging prospects for survival of many species of vertebrates; and yet it is the most relatively available source of protein in many areas. The taste for bush meat as a delicacy in affluent extra-tropical cen-

ters such as London is also a driving force for its illegal export, as is the expectation that lumbering and other working crews in the field in Africa will provision themselves.

Gathering plants in nature can be equally damaging, especially in view of the enormous quantities of herbal remedies and dietary supplements that are being exported to Japan, Europe, and the United States. For most of the people of China and India, which have a combined population of about 2.4 billion people (of a world total of 6.3 billion), plants are their medicine. Only about 15 percent of the needs are met from cultivated sources, however, and the impact on native plants that are used in this way can easily be imagined. Middlemen generally buy their supplies from those who scour the countryside to gather them, making substantial profits in the process.

A third very important driving force for extinction is the growing worldwide spread of aggressive, invasive alien species of plants, animals, fungi, and microorganisms. Thus, about a third of the species of plants in the northern hemisphere are estimated to be endangered or threatened with extinction because of competition with introduced weeds. In Hawaii, about half the native species of plants are threatened or endangered, almost all as a result of the activities of introduced plants or animals. The introduction of avian malaria into the Hawaiian Islands together with the mosquitoes that spread it (there were no mosquitoes in the Islands originally) has been a very serious contributor to the endangerment and extinction of native land birds (review in Pimm 2001). In other parts of the world, various species of *Phytophthora*, an oomycete, have been introduced and wrecked great havoc. In many cases involving fungi and microorganisms, it is difficult to determine what the original ranges may have been because our overall knowledge of the groups is so poor. At any rate, one species of *Phytophthora* is endangering native scrub over wide areas of Australia, particularly in the southwestern part of the continent. Half the world away, sudden oak death, caused by another species of the genus, is killing large numbers of native oaks and other woody plants in California. Alien species continue to spread rapidly, and clearly will exert an even greater negative influence on natural communities in the years to come.

Recently, it has become evident that global warming will make the survival of many species problematic, even in the absence of other factors, and that the influence of global warming on natural populations will increase greatly in the near future. The mean global temperature is estimated to have increased 0.8° Celsius since 1750, the baseline, and most of this increase has taken place in recent decades. As the emission of CO₂ and other gases continues and increases as currently projected, global temperatures are expected to increase by an additional 3°C or more by 2050, and would in principle continue to rise indefinitely if we do not take steps to curtail them, according to analyses presented by the International Panel on Climate Change. Future temperatures will vary locally, so that mean temperatures in continental areas such as the upper Great Plains and Midwestern area of the United States are predicted to increase two to three times the average. The effects of increases in average temperatures on the distribution and amount of precipitation are unpredictable, but clear; as such further changes occur, the damage to biodiversity caused directly by the increased temperatures will be magnified. Regardless of what happens to local precipitation, increased temperatures alone will render many conserved areas unsuitable habitats for the organisms and communities for which they were established. Excellent analyses of the predicted fates of individual species have been prepared for South Africa and Australia, but we are just beginning to consider such effects, with much more information to be available in the near future (Thomas et al. 2004). Certainly it appears likely that habitats of many species will simply disappear as the climate shifts. For the lower 48 states of the United States, it is predicted that global warming will eliminate all habitats above timber line by the end of the century; similarly drastic changes are likely to occur in other biological communities unless energy policies are altered significantly in all nations.

On the basis of habitat destruction alone, it has been estimated that two-thirds of the species

of terrestrial eukaryotic organisms on Earth could become extinct by the end of the present century (Pimm and Brooks 2000). Such a rate of extinction would be equivalent to that which happened at the end of the Cretaceous Period, some 65 million years ago, but the extinction that our children and grandchildren are likely to witness will have been caused by the activities of one species acting alone — the direct effect of human activities. Because this estimate is based on habitat loss alone, the other factors just enumerated can only make it much more severe. Of these factors, global warming is perhaps the least predictable and at the same time potentially the most damaging factor. It is important that additional analyses be performed so that we can deal with the consequences of global warming on biodiversity much better than we do at present, and then act on our findings. Another consideration of general importance is that biodiversity certainly cannot be preserved well in parks and reserves alone. We must learn to promote and understand concepts such as “country-side ecology,” proposed by Gretchen Daily and her colleagues, and “reconciliation ecology,” proposed by Michael Rosezweig, and to care for biodiversity effectively in the full range of habitats in which it exists.

At any event, all these negative trends taken together lend an urgency to charting and saving biological diversity that could not have been imagined just a few decades ago. Many papers in this symposium reflect ways in which this effort can be expedited and the quality of our collective effort improved. It is, however, also important that we biodiversity specialists, being well informed both about this situation and its consequences, help to provide adequate information both to our fellow citizens and to those who make political decisions that affect the future of biodiversity.

It follows from the considerations just presented that the preservation of biodiversity depends on conserving it to the extent possible wherever it exists, including urban areas. In addition, the traditional goal of preserving parks and other natural areas as repositories of biodiversity remains an extremely important strategy in any overall plan that might be conceived. The United States has been a global leader in this effort, and has done a great deal to help other nations establish equivalent protected areas for their own biodiversity. The passage of the Endangered Species Act in 1972 has provided a cornerstone of our subsequent activity in preserving biological diversity, and for plants especially cultivation in gardens and preservation in seed banks, followed in principle by re-introduction in nature, has been an important supplementary conservation activity.

In dealing with invasive species, many strategies must be employed in controlling them where they have been introduced and in preventing further introductions to the extent possible. This will involve increased inspection activities at national and other borders as well as the cooperation of industries such as marine and other shipping, the nursery and landscaping industries, and many others.

PROSPECTS FOR PRESERVING BIODIVERSITY

For the preservation of biodiversity overall, however, it will be necessary greatly to improve international understanding and cooperative international activities. As mentioned above, we are using the sustainable productivity of the world at 120 percent of the level at which our current rate of consumption can be sustained. To achieve sustainability for our planet as a whole, and thus protect the unique planetary resource on which we depend, it will be essential for those of us who live in the industrialized countries to form close bonds with all others and help everyone to move to sustainability together. Our realization that sustainability is a global problem, however, is only about 30 years old, and the degree to which we are willing to act on the situation remains problematical. As long as we live in a world that is deeply divided between the haves and the have-nots, with wealth and scientific expertise highly concentrated in a few countries, we have no chance of attaining global sustainability.

We who are scientists and engineers know well that expertise in our fields makes it possible for a nation to adopt the findings of others in the same areas, which mean so much to economic progress in our time. In addition, such expertise allows individual nations to use their own national resources in the best possible and sustainable ways, based on their own experience and knowledge. Unfortunately, there are more than 150 countries that have only a few such specialists, and these nations constitute about 40 percent of the world's population, mostly in areas of high biological diversity. More than 10 percent of the world's scientists and engineers practice their professions in India, Brazil, China, and Mexico, which collectively have about 40 percent of the world's population, and almost all of the remaining 90 percent live in industrialized countries, which collectively are home to less than 20 percent of the world's people (Population Reference Bureau statistics). It is no surprise that these industrialized countries also control such a substantial majority of the world's wealth, and cause a nearly equivalent proportion of the world's pollution, directly or indirectly. Ultimately, the preservation of biodiversity depends on understanding and managing the world sustainably. Conservation cannot be achieved by itself, because there cannot then be enough room, time, or resources to save so many species.

As biologists, we need to be a very concrete part of the overall solution, an obligation that our knowledge places on us. Certainly, collaborative research projects, participating in the training of scientists and engineers from developing countries, and working to insure that they have positions in which they can use their knowledge for the improvement of human knowledge and the benefit of their own countries are important. But we can also be internationalists and inform all groups of whom we are members of the importance of all countries around the world to us. With some 4.5 percent of the world's people, the United States consumes 25 percent of the world's resources and produces about an equivalent amount of pollution, which is enough to link us firmly with all other countries on Earth, regardless of how we decide to deal with that relationship.

In the 1960s, René Dubois devised the maxim, "Think globally, act locally." No matter what our profession, we can contribute greatly to the attainment of sustainability worldwide by paying attention to and caring for the environment around us — the parks and green spaces, recycling efforts, conservative use of energy, including renewable sources of energy, and many other aspects of sustainability that affect us personally and our daily lives. People in developing countries do not, by and large, have nearly as much impact on the environment as each and every one of us who live in industrialized countries, and we must look to our own individual demands and style of living if we wish to move toward the implementation of global sustainability. If nearly every one of us wishes to, and plans to, consume more resources than we do at present, and would like to have a better house, more money to send our children to universities, a better car, nicer vacations, and so forth, it is not realistic to expect governments or corporations to assume a "no growth" policy, or work towards the creation of a sustainable world in a less materialistic way. To arrive at that point, we need to consider why we in the United States use twice as much energy per capita as any other country on Earth, and why the standard of living in countries such as Switzerland, Sweden, or Germany is then approximately the same as ours. The only viable reason to be an optimist in the modern world is because of our individual determination to do something about the great problems that face us, and the privileges that we enjoy demand that we do nothing less. Participation in the political process is extremely important, because there is often no other way to achieve solid results in these areas.

The world is apparently not coming to an end, but it may offer people very different opportunities in 2050 or 2100 than it does now, its nature depending very much on the actions we take now, during the period when explosive growth in population and consumption levels has brought what may be the most destructive phase in the history of mankind on this Earth. The opportunities avail-

able to us now are, by definition, greater than they ever will be in the future, and we must take advantage of them while this is still possible. My overall point is that anyone who cares about the future of biodiversity in the world must also care about, and work for, the establishment of a sustainable world.

Biodiversity is extremely important to our future and that of our fellow citizens, regardless of how they may view it individually. Our food, much of our medicine, our building materials, and, in the early years of understanding molecular biology, our understanding of how genes function and our sources of new genes — these all depend on biodiversity. Understanding it, enjoying it, conserving it, and appreciating it as the single unique factor that makes life possible on Earth. No one could possibly predict where our understanding of biology will take us in the future, but no one can doubt that conserving as much as possible of the biodiversity as we possess now is a highly desirable strategy regardless of what our motivation may be. And that is why it is important for us to become active not only in the study of biodiversity, but also in its preservation through the contributions we can make to a sustainable planet.

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TAXONOMY

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**Presented on the campus of San Francisco State University
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**Arranged and edited by
Michael T. Ghiselin and Nina G. Jablonski
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Introduction

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The six papers published here were presented in the symposium, “The Future of Taxonomy,” on June 18, 2003 as part of the celebrations for the 150th anniversary of the California Academy of Sciences. The symposium was presented at the annual meeting of the Pacific Division of the American Association for the Advancement of Science in June 2003 at San Francisco State University.

Although it was not planned that way, all of the papers focus upon a common theme. Our practices of classifying and naming, which go back to Linnaeus and even earlier, were undermined by Darwin and today seem on the verge of collapse. Various changes have been suggested, including going so far as to abandon both binomial nomenclature and categorical rank. The PhyloCode, which would effect such changes, is a good example of proposed reorganizations.

Michael Ghiselin treats classification as the organization of knowledge, and on that basis provides a broad overview of the philosophy of systematics. He explains and updates the idea that species are concrete, particular things (individuals) rather than abstract kinds of things (classes). Treating the species category as a natural kind with its own laws of nature forms the basis of an argument in favor of having one and only one species concept. That argument could be used to justify having at least one rank.

Charles Godfray treats taxonomy as information science, and provides an irreverent view of both past and current practice. Although critical of what some consider the vices of the subject, he suggests that much of traditional practice might be maintained, and expresses skepticism about some of the recent proposals, including the PhyloCode. As he sees it, the situation calls for the creative application of computer technology.

Peter Forey takes a new look at Linnaeus, and asks whether he has much relevance for us moderns. The discussion seems timely, because the current approach — with its binomials and categorical ranks — largely derives from him. Forey suggests that we should maintain some of the older practices. In effect, he advocates keeping ranks, but not taking them seriously.

Kevin de Queiroz treats species as lineages, and on that basis seeks to unify the diverse views about that category. His views are somewhat different from Ghiselin's, but the idea of treating taxa as lineages is consistent with their individuality and is widely accepted. It is also the basis for discussion of how we name taxa, something to which both Ghiselin and de Queiroz have given a great deal of thought, and something that is discussed in more detail in the remaining two papers.

Mikael Härlin tackles the problems of how we name taxonomic groups. If populations and lineages are individuals, their names are proper names, and have no defining properties. One can fix the reference of the name by “pointing” at the common ancestor, but there is a serious tradeoff here. Although we are provided with a strictly objective way to attach a unique identifier to a lineage,

our idea of what that lineage is may change through time. Therefore, as science evolves we will find ourselves using the same name for different things.

Alessandro Minelli, who has been much involved with the International Code of Zoological Nomenclature, discusses the "legalistic" significance of taxonomic publications. He gives reasons for changing the rules, and also for coming up with a more modern way of linking the taxon's name to the taxon itself and to the scientific literature.

Taken together, the six papers all point in the same general direction. Taxonomy is re-examining its practices, even with respect to such central activities as bestowing names upon the formal units in classification systems and the methods of dissemination of taxonomic information. We are in the midst of a lively debate, the outcome of which is hard to predict. However, it seems inevitable that there are some important changes ahead in the future of taxonomy, and that many will be driven by the growing market outside of systematic biology for taxonomic information. Binomial nomenclature and categorical rank may be abolished altogether. Alternatively, traditional practice may be maintained, perhaps with more modest adjustments. In either case, taxonomy will be cultivated with a better understanding of its goals and practices.

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Taxonomy as the Organization of Knowledge

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The goal of taxonomy is the same as that of classification among the sciences in general: the organization of knowledge. Such knowledge is the intellectual content of the science and should not be confused with the organization of tools used in work. The new philosophy of systematics that emerged in the second half of the twentieth century clearly distinguishes between groups that are concrete particular things, or individuals in a broad ontological sense, and those groups that are kinds of things, or classes. In modern taxonomy the taxa such as *Homo sapiens* and *Homo* are individuals, and the categories such as the species and the genus are kinds, or classes. The laws of nature refer only to classes, not individuals and for that reason the categories but not the taxa can be considered natural kinds. Taxa having the same rank are equivalent insofar as they play the same role in nature and in evolutionary theory because they participate in the same processes and the same laws of nature apply to them. Species are fundamentally different from higher taxa because above the species level cohesion is lacking and the units are purely historical entities. Species are fundamentally different from lower taxa because below the species level cohesive capacity still exists. Asexual clones are likewise not cohesive and should not be confused with species and lower taxa. The kind of pluralism that allows the coexistence of a diversity of species concepts creates confusion by using the same term for fundamentally different kinds of objects, impedes the unification of knowledge, and turns taxonomy and its branches into parochial disciplines that offer little of anything of interest to science and intellectual culture in general.

Systematics, or systematic biology, has commonly been defined as the science of organic diversity, and taxonomy as the branch of systematics that deals with its more formal aspects, especially classification schemes and nomenclature. Classification and naming of course are by no means limited to biology, or even to the sciences. They are fundamental to language and thinking in general. This discussion studiously ignores such semantic niceties as whether a system in which the elements are individuals rather than classes should be considered a classification (Griffiths 1974; O'Hara 1993). Let us rather focus on the things rather than the terms. A proper understanding of classification in general and taxonomy in particular is better gained by considering its function in the life of the mind.

My earlier thoughts on such matters suggest that the goal of classification in biology is the same as it is in all sciences: the organization of knowledge (Ghiselin 1997:17, 24, 300). Scientific knowledge has to do with the intellectual aspects of our lives — with causes, theories, history and the laws of nature. We scientists organize our knowledge in order that we can think, and indeed if it were not organized it would not be knowledge. We also organize other things, such as laboratories, expeditions, and museums. It does not seem a good idea to treat a grocery store as a model for

how scientists ought to classify or to use such an arrangement of goods as an argument in favor of classification on the basis of similarity as suggested by Mayr and Bock (2002). Yeast in a grocery store is not put next to mushrooms, whether fresh, canned, or frozen, and roses are not close to strawberries. When doing research, I avoid paraphyletic taxa altogether, but I find them perfectly innocuous when filing my reprints.

There is an important difference between the organization of work and the organization of knowledge, even when the work is organized so as to further the acquisition of knowledge. Confusion between the two has had some unfortunate consequences, especially with respect to the "practical" aspects of taxonomy. Mayr (1998:9722) gets his priorities wrong when he asserts:

A-classification is an information storage and retrieval system. Its aim is to permit you to locate an item with a minimum of effort and loss of time.

Of course, classifications are useful for that very reason, but there is a profound difference between knowledge and information. A scientist knows a great deal, whereas a telephone book knows nothing whatsoever. Scientific classification therefore must not be treated as if it were just epistemological gadgetry. It tells us what kinds of things we are dealing with, and therefore it is an ontological affair. Science is about the things and kinds of things that play a role in scientific laws and theories, and that is what gives meaning to its classifications.

Our ontology, in other words, our conception of what things are, and therefore of what is responsible for their properties, has evolved, together with the rest of science, profoundly affecting our conception of how we ought to classify. Biological classification was revolutionized in the nineteenth century when the natural system that had been codified by Linnaeus was reinterpreted in evolutionary terms by Darwin. It was revolutionized again in the second half of the twentieth century when the philosophy of the subject finally caught up with its practice. The traditional answers had to be rejected because they had addressed the wrong questions. By the dawn of the present century there had emerged what I have called the "biological consensus" and the "philosophical consensus" with respect to species concepts (Ghiselin 2002). By "consensus", I do not mean to imply that the views in question are uncontroversial, but rather that they are the majority view and there is no satisfactory alternative to either of them. By the biological consensus, I mean that species are the most incorporative populations that participate in evolutionary processes. By the philosophical consensus I mean that species are not classes or kinds of organisms (or of anything else), but rather individuals at a higher level of integration, the component organisms of which are their parts, not their members. In logical terminology this implies that the taxonomic category of the species is a kind, the members of which are individual species (in other words species-level taxa).

The "individuality thesis," which is the core of the philosophical consensus became a serious topic of debate among biologists and philosophers around the time that I finally managed to get it taken seriously (Ghiselin 1974; Hull 1976). A remarkable variety of objections to it have appeared. The arguments have been laid out in great detail in my recent book (Ghiselin 1997). Therein I answered all of the objections to it that had appeared in print up to the time the book was written. I see nothing in subsequent publications that presents a viable alternative. But efforts go on apace and there is room for some further commentary. One topic of interest has been the possibility that species are natural kinds. I reject that view, but the notion of natural kinds provides a basis for an argument against what is called "pluralism" with respect to species concepts. This argument has been sketched out earlier (Ghiselin 2002), but only briefly.

Perhaps the best way to explicate the individuality thesis is by reference to a scheme of the familiar Linnaean Hierarchy with its groups and levels:

<i>Classes</i>	<i>Individuals</i>
Phylum	Chordata, Mollusca, etc.
Genus	<i>Homo</i> , etc.
Species	<i>Homo sapiens</i> , etc.
Organism:	Charles Darwin, Fido, etc.
Cell	etc.
Molecule:	etc.
Atom	etc.

Actually the levels from the organism downward are not part of the formal taxonomic scheme, but that is irrelevant for my point. To say that *Homo sapiens* is a species is equivalent, at a lower level, to saying that Charles Darwin was an organism. The individuals (on the right) have parts at lower levels, unlike the classes (on the left). Sorting out the classes and individuals in this way makes it easier to explain certain important points. A species concept or definition is a definition of the name of a class ("species") not a definition of an individual that is an instance, specimen or example of the class of species (such as "*Homo sapiens*"). By analogy, an organism definition is a definition of "organism" not of Charles Darwin.

Maybe this is not clear enough, so let us take a brief look at some political individuals classified in the same manner:

<i>Classes</i>	<i>Individuals</i>
National/State:	Canada, Mexico, etc.
Province	Ontario, British Columbia, etc.
County	Ontario County, York County, etc.
City	Ontario, Toronto, etc.
Citizen	Janet Landa, etc.

Didactically, this analogy has often proved quite useful. Obviously, Ontario is a province and not a National State. Also, Ontario is a part of Canada, not a Canada. Janet Landa, although a Canadian, is not a Canada either. By the same token she is a part of *Homo sapiens*, rather than a *Homo sapiens*, whatever that is supposed to mean. Now consider why is it that we rank entities at the same level. For the citizen that is more or less obvious: each functions the same way and that is even true from one national state to another. It is a bit less obvious why Canada is equivalent to much smaller and less populous national states, such as Luxembourg. The answer is their sovereignty. More problematic is the equivalence between the subunits of various national states, for example, between Manitoba and Rhode Island. Here again we have an important point: the categories may give just quantitative rather than qualitative distinctions. There are serious alignment problems here.

Crudely speaking, a natural kind is a class the membership of which is determined by laws of nature (Quine 1974, 1979). A good example would be the various chemical elements. Supposedly a piece of metal is gold because it has the atomic number 79 and other important properties that make it gold rather than lead. Natural kind theory can be understood as an effort to ground classification in causality (etiologically, see Ghiselin 1997, pp. 74, 191), and in that respect it resembles efforts by modern taxonomists to create natural systems, although the underlying causes differ profoundly. Scientific investigation would then aim to discover the underlying causal basis of groups that are already to some degree known, but not fully understood. Accordingly, the laws are often conceived of as essences, or something close to essences. That makes sense if we understand what natural kind theory was supposed to accomplish with respect to definition (Kripke 1977, 1980). It meant that one could define, or fix the reference, of the name of a class through a so-called osten-

sive definition, without having to provide defining properties. That made the definition of the names of classes very much like that of the names of individuals. We point at the single thing to be named, and that fixes the reference of the name.

An appreciation of the fact that species and lineages are individuals has given rise to much fruitful discussion on how to "define" the names of taxa by stating which lineages it is to which the names refer, and without pretending that such taxa have defining characters (De Queiroz and Gauthier 1990, 1992, 1994; De Queiroz 1994). The suggestion that the names of species must be defined ostensively was one of the first important implications of the individuality thesis for the practice of taxonomy (Ghiselin 1966:209). It clarified the role of nomenclatorial types. The PhyloCode, a further development of that line of reasoning, is something for which I am happy to accept some of the blame but not the credit! Ostensive definition works very well for individuals, including species and lineages of higher rank, but it runs into serious difficulties when we try to apply it to classes. Until the laws that supply the causal basis are known, the natural kind term has to be a "something, I know not what." And once we have discovered what the laws are, we can replace the ostensive definition with one cast in terms of defining properties.

However, the idea that the classes of interest to scientists are the ones that owe their important properties to laws of nature remains attractive. Pre-Darwinian biologists widely believed that taxonomic groups are manifestations of as yet unknown laws of nature. Darwin, however, showed that they are purely historical entities, the products of contingency, not of nomic necessity (as such conformity to law is called). That makes an enormous difference. Laws of nature make no reference to any one individual but rather are about classes, which are spatio-temporally unrestricted. So to make species and other taxa into natural kinds one would have to deny that they have a beginning or an end, a particular location, and much else besides. Given that species are individuals, then the laws of nature would have to be about classes of species, such as big species or inbred species. I have at least come up with some examples of laws for classes of species. Some authors have claimed that species are indeed classes and have asserted that they do have laws (Mahner and Bunge 1997; Bock 2000). No example of such a law has been provided. Don't hold your breath.

Species are not classes of organisms. However, like multicellular organisms, they are individuals with somewhat homogeneous components. That homogeneity is one obvious reason why species are so often mistaken for classes. It also has made it easier for philosophers to perpetuate the delusion. The laws of nature are predictive, if only on a statistical basis and with all sorts of qualifications. One might claim that certain properties of the components of a taxon can be extrapolated to other pseudo-instances of that taxon. Of course one can, much as with an individual organism and its components, or with its ontogenetic stages. One can characterize a species by its chromosome number, and there is even less chromosomal variation within an organism. Likewise a person's personality, although it may change with the passage of time, is usually stable enough that we can forecast some kinds of behavior. When systematists are studying phylogenetics they try to find so-called "conservative characters," which are parts that evolve slowly and therefore are more reliably extrapolated across time and genealogy. But such extrapolation, to the extent that it is based on laws of nature at all, is not based upon laws of nature that refer to any of those individuals. The notion that biological classification is "predictive" has some justification, but only in the sense that familiarity with somebody's personality allows one to "predict" his behavior.

The notion that species are natural kinds is hardly new (Kitts and Kitts 1979). The arguments against it are well known (Hull 1981). Its latest manifestation takes the form of asserting that species are "homeostatic cluster natural kinds" (Boyd 1991, 1999; Griffiths 1997, 1999; Keller et al. 2003). Calling species natural is unobjectionable. Species are natural objects, not something that has been created through human artifice. Natural classification remains natural classification irre-

spective of whether the groups are classes or individuals. However, "homeostatic" is a bad metaphor. If something is to have homeostasis in the literal sense it has to be an individual, such as a thermostatically controlled heating system or a homeothermic organism. Boyd argues that species possess something like homeostasis, and they do, but that is because they are individuals not kinds. To say that species are kinds is simply a category mistake. They do not function as kinds in evolutionary theory (Coleman and Wiley 2001) and that is all that matters. Consider two metaphysical taxonomies:

I.

That which is not natural

Artificial kinds

Supernatural kinds

That which is natural

Natural kinds that are kinds

Natural kinds that are not kinds

II.

Individuals

Kinds

Natural kinds

Artificial kinds

The former classification is what we get when we conjoin bad metaphysics with bad nomenclature. Rather than belabor such points, however, the goal here is to turn the argument on its head, and rebut those authors who claim that species are natural kinds and who on that basis argue that we should adopt a kind of pluralism with respect to species concepts.

With respect to natural kinds, my argument is as follows. The biological species (category) is a natural kind. It has laws of nature that apply to those individuals that are its members. It is, however, one of many levels in the hierarchy. Other levels are different kinds, and different laws of nature apply to their members. This is because the individuals at the various levels participate in different processes. Not surprisingly, they play different roles in evolutionary theory. If we pass upward in the scheme of the Linnaean hierarchy sketched out above we can easily see that the individuals at each level engage in somewhat different processes, though some processes do go on at more than one level. Atoms form covalent bonds; cells undergo cell division; organisms copulate; and species speciate. Note that above the species level, something very important happens, or ceases to happen. Cohesion ceases to exist, and we get purely historical entities that do not participate in processes at all. Matters may be a little more complicated, but the basic point remains. At that level there is a fundamental discontinuity in the causal nexus. This is appreciated in the theoretical literature. Gould (2002), who belabored the individuality thesis at great length, came to recognize that species selection will not work above the species level. At populational levels below the species analogous processes do go on, but obviously not among pseudospecies for these, being asexual, do not consist of cohesive populations. Wiley (1978) even suggested that noncohesive individuals are not individuals at all. I, on the other hand, have always argued that such a move does not make quite the proper ontological cut in metaphysical taxonomy (Ghiselin 1981, 1997). In other words, instead of:

Classes

Individuals

Historical entities

I prefer:

Classes

Individuals

Cohesive individuals

Historical entities

I refer to an "ontological cut" as a deliberate allusion to Plato's metaphor of cutting nature at her joints (see his dialogue *Phaedrus*). In metaphysics, as in any other natural science, the goal of classification is to arrange the materials in terms of their fundamental relationships one with another. The distinction between classes and individuals is arguably the most fundamental that one can make. Those individuals which are, and those which are not, cohesive, nonetheless share a residuum of very important properties that classes lack: they have a beginning and an end; there are no laws of nature for them, etc. But the two kinds of individuals are indeed fundamentally different in a very important way, and that difference is profoundly significant for how we ought to classify. Once a species has speciated, it becomes a purely historical entity, and like all purely historical entities it is no longer capable of participating in processes, in other words of doing anything. Exactly the same is true of clones and other entities that have lost their former cohesion. The reason why the species category is so important, and so profoundly different from other taxonomic categories, is that above the species level the individuals play a profoundly different role in nature and in our ways of thinking about it. And by the same token there is no excuse for classifying in a way that does not underscore the distinction between species and pseudospecies. Asexual species are a contradiction in terms in every context in which the species concept plays a role in evolutionary theory. In this connection, I should mention that there has been a great deal of misconception and outright mythology about bacteria. If bacteria do not have sex, why did Joshua Lederberg get the Nobel Prize for discovering it? And why has molecular research so clearly shown it to be rampant among them? The problem that bacterial sex poses for speciation theory is not that it does not exist, but rather that it may not be so effective a cohesive force as it is among eukaryotes and, therefore, not limit diversification to such a great extent (see Dykhuizen, this volume, p. 54).

Likewise, the populational components of species differ from entire species in a fundamental way. Therefore, they play a different role in evolutionary theory, albeit not for the reason that species differ from higher taxa. If parts of species that have been separated geographically for a time come back together they fuse back into a single population, owing to the forces of cohesion. In evolutionary theory, allopatric populations that are not yet reproductively isolated function only as incipient species. It is unfortunate that the question of what qualifies as a species has been cast in terms of the amount of gene flow. For that reason as well, it is sometimes wrongly assumed that there can be no gene flow at all. Provided that gene flow does not suffice to make the populations in question fuse back into a single unit and prevent them from diverging indefinitely, they are separate species. (For a detailed exposition, see Ghiselin 1977:99–102).

Of course, parts of species, and parts of organisms are important, but nobody has ever provided a legitimate reason for calling them species. I emphasize this point because certain pluralist philosophers have alleged that there are certain contexts in which it is more appropriate to use a species concept other than the biological one (most recently Reydon 2003 and Brogaard 2004). So far as I can tell, this allegation is nothing more than a figment of their imaginations or an expression of hope. I can give plenty of examples where confusing species with other things has had a detrimental effect on biological research, and when not doing so has had a beneficial effect, sometimes saving countless human lives. The value of distinguishing among the various cryptic species of mosquitoes, some of which serve as vectors of malaria and some of which do not, is a particularly well known example of the latter. But I can think of not a single case for which our study of

those other things would be in any way ameliorated by calling them species rather than something else. Maybe somebody else can think of one. However, it seems to me that unless the pluralists can come up with some good examples that the rest of us can examine critically, we ought not to take them seriously.

The reason for having the units of evolutionary history correspond to those that are used in the study of evolutionary mechanisms may not be intuitively obvious to everybody. Although there are no laws of nature for individuals, there are laws of nature for kinds of individuals. Prior to the emergence of the new philosophy of systematics it was widely maintained that there are no laws of nature in biology, and that, therefore, biology is somehow an inferior kind of science. It turns out that biology has its laws of nature, but these are laws for kinds of species, and for other kinds of individuals. As effective population size goes down, the frequency of loss of alleles by drift goes up, for example. Such laws have long been implicit in evolutionary biology, but they were overlooked because nobody knew where to look for them. Biology, like astronomy, is about both history and the laws of nature. In both sciences, our classification systems need to be organized in such a manner that the two can be put together. Data, including historical data, about particular things are used to test hypotheses that involve laws about things in the abstract. And laws are used to explain and to predict the behavior of the things to which they refer. We can begin if we wish with the Big Bang and provide a scientific narrative account of the formation of galaxies, stars, planets, and life with all its components.

We can see why it is not so good an idea to have a species concept, or, if you prefer, a definition of the species category, such that it conflates species with parts of species. In organizing our knowledge, we want to keep entities that play different roles both in nature itself and in our thinking about it conceptually distinct. We do not want to confound an organism with one of its component organs, or an atom with a subatomic particle. However, we do want to arrange the materials in our classification so that the individuals to which the same laws of nature apply are members of the same natural kind. That means that a species should be precisely the same kind of thing whether we are doing taxonomy, ecology, or genetics. Of course, a given process may occur, and the same laws of nature may apply, at more than one level. There are processes and relevant laws of nature that apply to populations generally, including parts of species as well as entire species: natural selection, sexual selection, genetic drift, to list but a few. We should also note that an individual can be a member of more than one level in a hierarchy, for example, a unicellular organism. In theory, a species might consist of just one self-fertilizing organism, and conceivably that organism might be the common ancestor of two species isolated by virtue of different chromosome numbers. That, however, would not contradict the proposition that it is species, not organisms, that speciate.

Species don't just speciate. They become extinct. And they also resist extinction. Why should we treat species as particularly important units when we aim to conserve biodiversity? The individuality of species helps to make some of the considerations more explicit. Although species are not organisms, they are like organisms in some important respects. When a species becomes extinct it is lost forever, and in that respect extinction is just like the death of an organism. How about the extinction of a part of a species? There is some analogy with the destruction of a part of an organism. A lost organ can be replaced through regeneration, and something like that can happen within species through migration and genetical recombination. In other words, a species has an ability to resist extinction over and above that of its component subpopulations.

For effective interdisciplinary work, the various systems need to be compatible with one another. One cannot carry out an effectual research program in comparative biology if the things being compared are not equivalent. Paleontologists devoted a great deal of effort to counting numbers of families and other taxa of higher categorical rank in the fossil record, but in the absence of

a genus concept there is a serious question as to what, if anything, was being quantified. In principle, there is no such problem of commensurability in studies of biodiversity at the species level. However, the species concept has to be properly applied. In certain taxa, especially marine ones, a failure to recognize cryptic species has led to an underestimation of the number of species by a factor of ten (Knowlton 1993, 2000). The result has been a serious misunderstanding of both the generalities and the particulars of speciation, and not just inaccurate estimates of biodiversity. If the so-called species have to be morphologically distinct and easily told apart, then we get the impression that speciation involves a kind of saltation, or that we have before us a legitimate example of speciation in sympatry, or perhaps that the genus that we are studying is a very diverse species.

Just as taxonomists revise their classifications as a greater sample of biodiversity accumulates, so too do they reconsider the fundamental principles on the basis of which they classify. The notion that classification is based on similarity is an epistemological myth, and one that could only be corrected by ontological considerations. It was evolutionary theory, with its historical ontology, that led Darwin to reject that notion altogether and insist that classification be strictly genealogical. It was likewise ontological considerations that led Dobzhansky and his contemporaries to bring species level taxonomy into harmony with the genetics of natural populations. Finding a theoretical and philosophical basis for coordinating the basic units of taxonomy with those of other branches of biology, and with those of other sciences as well, seems a promising way to carry on in that grand tradition. Given past success and present prospects, the future of taxonomy looks bright indeed.

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Taxonomy as Information Science

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The taxonomy of a group of organisms today consists of the sum of papers on their classification in a myriad of different journals. This distributed taxonomy, however, is not the only possible model. For a particular group, species descriptions, keys, consensus and alternative classifications, and references to type material could all be mounted on the web to provide what might be called a unitary taxonomy. Once established, future work on the group would refer only to the species and other taxa hypotheses on the unitary web site and not to the preceding paper literature. The paper will explore the advantages and disadvantages of unitary taxonomies. The advantages include greater accessibility and visibility, preservation of the useful but not the hindering legacy of the past, the ability to employ greater numbers of images, and the ease of linking morphological and molecular approaches. The disadvantages include the costs of maintaining unitary taxonomy web sites, the requirement of web access, and the risk of authoritarianism. I argue that the advantages outweigh the costs and that unitary taxonomies may be the means of attracting the new funds that systematics so urgently needs and deserves.

Why do modern developed societies pour so much money into scientific research? In some cases the answer is straightforward, there is a clear economic benefit in the short to medium term. This is the reason for some government and most industrial funding. There may also be non-economic short to medium-term benefits that can be thought of as improvements to our quality of life. How can we disperse oil slicks, or improve air quality by better scrubbing power station emissions, or develop better forms of medical care (medical research has both economic and non-economic short-term aims)? All of these can be justified and accounted for by rational-choice economics using straightforward and easily communicated concepts of utility.

This, however, accounts for only a fraction of the activity in our great research institutions, universities, museums, and other research centers. Here, much of the research has only long-term potential benefits; or is capacity building, paving the way for more utilitarian studies; or is “blue-skies”, with no identified concrete benefits to mankind but a hope that something unexpected and useful might arise; or is just curiosity driven, motivated by a belief that accumulating knowledge is somehow a noble human endeavor. There is a curious social contract between the citizen and the scientist that allows the latter considerable latitude in what he or she does with taxpayers’, charity-givers’, or philanthropists’ money, yet nevertheless demands certain some ill-defined returns for whatever type of science is funded.

Where does taxonomy fit into this picture? Some taxonomists can point to direct short- to medium-term benefits of their work. The value of fossil stratigraphy to the oil and mining industries is an obvious example, as is the importance of entomological taxonomy to biological control for pest management and — although often exaggerated — plant taxonomy to bio-prospecting. But these are a minority; few businesses employ taxonomists as part of their core enterprises, and pri-

vatising taxonomy would be a disaster. The short- and medium-term goals of taxonomy relate to quality of life than rather wealth creation. Where taxonomists are employed or used as consultants by industry, it is more typically in their environmental units, which require expertise in assessing negative effects of their activities on the environment. Governments and NGOs also often use taxonomists in this capacity.

But all of this accounts for only a small fraction of taxonomy — the justification for the remainder lies in the realm of capacity building, “blue skies” and research driven by curiosity. Of these, “blue skies” is perhaps the least persuasive, at least as I define it here as research that may trigger unexpected benefits to society. Though it is rather nonsensical to say one cannot think of any unexpected benefits, the history of the subject is in delivering research along predicted rather than unpredicted lines. The argument for the importance of taxonomy in enabling other science is unimpeachable. Much of whole-organism biology requires the accurate identification of species and, increasingly, an accurate understanding of their phylogeny. This is perhaps most critically true in community ecology, the science of the interaction of assemblages of different organisms. The lack of good taxonomies for many groups of especially tropical organisms is a real impediment to research. It is not only the supra-organismic sciences that benefit from taxonomy. One must be careful not to exaggerate but an increasing number of interesting questions in molecular, genetic and developmental biology are benefiting from a comparison across species, especially when the comparison is based around an *Arabidopsis*, *Caenorhabditis*, *Drosophila* or other model organisms.

In my view, an unarguable case can also be made for curiosity-driven taxonomic research, of a type that will command public support. One line of reasoning, the one I find the least convincing, is that the human species has a duty to document the biodiversity with which it shares the planet. I think “duty” and similar expressions are philosophically suspect and really just a cover for a powerful emotional need to understand and conserve plants and animals. E.O. Wilson would call this emotion part of our species’ “biophilia” and I think that it is this type of notion, shorn of the highfaluting rhetoric of duty, and genuinely democratized so that it is much more than the special pleading of taxonomists and fellow travelers, that is the strongest justification for continued and increased support for taxonomy. That this ground swell of support for the subject is real is evidenced by the legion of amateur taxonomists (in which category I include keen bird watchers and wild flower enthusiasts, and perhaps largest of all, serious amateur gardeners) and the popularity of programs and books with significant taxonomic content (I’m reminded here of a six-year old girl I know who has an encyclopedic knowledge of dinosaur nomenclature).

Thus, is there a problem in taxonomy and, if so, what is it? I think there is a widespread belief amongst many taxonomists and scientists who use their output that species-level taxonomy is under-funded and failing to produce the systematic work needed by other fields. I am most familiar with the situation in the United Kingdom where the evidence for this is clear. Descriptive taxonomy has largely disappeared from the university staff room (and curriculum) while funding for major museums and herbaria has fallen in real terms. The Linnean Society, the Systematics Association, and similar societies produce manifestos lamenting this decline, and government responds by setting up serial enquiries (the latest at <http://www.parliament.the-stationery-office.co.uk/pa/ld200102/ldselect/ldsctech/118/11801.htm>) which do some good (one led to a five-year taxonomy initiative by a research council) but lead to nothing permanent and structural to reverse the situation. I think similar things have happened in other countries, a steady decline with some encouraging exceptions (for example, the couple of recent National Science Foundation taxonomic initiatives in the United States). Most pernicious of all, the standing of the field has become undermined, with taxonomy thought of as “old-fashioned” as and less sexy than the many

other disciplines that make up modern biology. I have concentrated here on species-level taxonomy; the standing of phylogenetics is somewhat higher, though this too suffers from the lack of funding for the whole field.

Here is an argument for funding less taxonomy. Scientific research is essentially a market and, give or take a little inertia and the minor distortions of fads and fashions, funding follows the questions that are either most useful or most interesting. In an environment where for quite healthy reasons there is intense competition for the research dollar, the lack of resources going to the subject is a logical and helpful response to changing economic and intellectual priorities. Taxonomists feel under-funded only because they remember a bygone age when they were at the cutting edge of science.

Clearly this argument is simplistic, and no one would seriously argue that an invisible hand is creating a perfect market to guide research funding. But there are some features of the modern science-funding scene that do resemble a market, and in this article I want to argue that thinking about how taxonomy operates in this milieu may help identify what changes the subject should make to increase its support, and what changes it should shun because they would do the reverse. Specifically, I want to concentrate on more long-term research and suggest that funds do tend to follow the most interesting questions but in a more sophisticated manner than that of the argument of the last paragraph. What matters is not only how interesting the question is, the potential extra science that the research may leverage, but how capable the subject is of delivering useful output. I think taxonomy is suffering not because it is any less interesting or important than it was fifty years, but because it is largely failing to deliver.

ARGUMENT BY ANECDOTE

The Alloxystinae are a group of tiny and fascinating wasps that are hyperparasitoids of aphids (and a few other Homoptera). They belong to the insect order Hymenoptera and are traditionally included in the paraphyletic Parasitica, the vast majority of whose members are parasitoids of other insects (Gauld and Bolton 1988). They are now normally placed in the family Charipidae of the superfamily Cynipoidea, whose most famous members are the gall wasps (Cynipidae) which have secondarily lost the parasitoid life style. Taxonomists consider there are six or so genera of which only two, *Alloxysta* and *Phaenoglyphis*, have more than a few species.

The biology of the aphid-attacking species is relatively uniform. Aphids are prey to many primary parasitoids, especially those belonging to a group of braconid wasps called the Aphidiinae. These lay their eggs in the aphid, typically before it is fully grown, and the parasitoid first-instar larva remains in a state of arrested development while its host feeds and grows to full size. The parasitoid then resumes development and consumes the aphid from the inside, causing it to become a husk, cemented to a plant surface. Inside this husk, or mummy as it is normally called, the primary parasitoid pupates. Aphid primary parasitoids are attacked by two guilds of secondary parasitoid, a taxonomically diverse group that lays its eggs in the primary after mummification, and the Alloxystinae. The latter do not attack the mummy, but live aphids containing larval parasitoids in arrested development. Using semiochemical signals, in a way that is not very well understood, the alloxystine is able to detect and distinguish a parasitized aphid, and then somehow to place its egg within the relative tiny body of the first parasitoid inside the aphid. The alloxystine first instar larva hatches and itself suspends development, resuming growth only when the primary parasitoid has caused the host to mummify (Sullivan 1988).

These wasps are important to us because for the last ten years we have been using aphids and their primary and secondary parasitoids as a model system to investigate general issues in commu-

nity ecology (e.g., Müller, *et al.* 1999). We are particularly interested in indirect effects: how the population dynamics of two aphids that feed on different host plants and so never interact directly may be coupled through their shared natural enemies (or, similarly, how two primary parasitoids that attack different aphid species may be linked by shared secondary parasitoids). To assess the potential for indirect effects we have built quantitative food webs each summer month of the last ten years of the aphid-parasitoid community in a field site in southern Britain (Müller *et al.* 1999). The web is used to design field manipulation experiments to test specific hypotheses about indirect effects (Morris *et al.* 2001). It is clearly important for us to get the taxonomy right.

Over ten years we have recorded about 40 aphid species from our site and about 30 primary parasitoid species. Of the secondary parasitoids, eight species attack the mummy, which leaves the Alloxystinae. At the start of the study, I thought that identifying the Alloxystinae would be relatively easy as there was a modern key to the British species. However, it was worrying that several long-series of reared specimens that seemed *prima facie* distinct (related hosts, morphology very similar) keyed out to the same species. Moreover, the only other alloxystine taxonomist in Europe maintained a much narrower species concept, though this was apparent only from notes and short papers as he had never attempted a Europe-wide revision. He used character states ignored in the British review which had sunk, without explanation, a number of species which he considered distinct. So which was correct, continental splitting or British lumping?

Frank van Veen joined my group from Holland and using a combination of molecular methods and careful study of morphology unambiguously, I believe, resolved this issue in favor of the continent. Sequencing the ITS region provided excellent distinguishing markers (van Veen *et al.* 2003), and based on this he was able to assess critically which morphological characters were most useful and hence write a traditional key. The British revision listed 16 species of *Alloxysta* from the United Kingdom while now we believe there are at least 18 in our food web (with at least another eight attacking tree-feeding aphids at our site that we do not include in the web). There were also some surprises, to our knowledge, the opening couplet of every key that has ever been written to *Alloxysta* begins with "wings fully developed/wings missing or shortened" or something similar, dividing the genus into winged or unwinged species. Frank found that four out of the five European unwinged "species" were in fact polymorphic, with all (two cases) or some (two cases) females winged. (The fifth species lives on the Arctic island of Svalbard; it has never been reared but presumably attacks the one species of aphid on the island, curiously, no primary aphid parasitoid has yet been found).

Van Veen's key initially included the species as codes, but he was soon able to assign about half the taxa to the few comparatively well known species, and with the help of Henk Evenhuis, the long-retired continental expert, to the species that he had studied over the years. But what of the rest? It was helpful that an American taxonomist had catalogued the names that had been applied to the world's Alloxystinae giving authors and, where known, the location of the type specimens. Many were telegraphically described by Keiffer in the early years of the twentieth century; while several species, secondary parasitoids of important pest aphids, had been described over and over again (Evenhuis had labored hard to sort out, successfully, many but by no means all, these problems). Were our species "v2, v3, ram1, br1, br2", etc. amongst these names floating in taxospace? More ambitiously, could we use our findings as a basis for a modern revision of the group?

The original descriptions and most early work (before Evenhuis) were essentially useless. Seldom were new species compared with others, and hardly ever were those characters described which today are recognized as the most helpful. The only way forward is to examine the types, distributed throughout the museums of Europe (with a few having found their way to the Smithsonian). Examining 100-year old alloxystine types is not fun (a referee of this article, correct-

ly, points out that this is a value judgement — but for the reasons that follow I claim it the status of a universal truth!). They look nothing like recent specimens, and usually have a washed out appearance that can make discerning critical characters almost impossible. Good bird watchers identify species by their “jizz”, the sum of the animal’s color, morphology and behavior, and entomologists who see many specimens of an insect species, even dead under the microscope, develop an equivalent skill. But while this is of huge value for recent specimens, it is rarely much use for studying old types. A different almost forensic approach is needed, the analogy seeming particular apt as often (>50%) the specimen is damaged, sometimes severely so. Moreover, frequently it is not clear what specimen actually is the type; it may be missing or poorly labeled, or several specimens may be mounted together, not infrequently of different species.

Sorting out this mess would be a huge undertaking, involving much travel, much scholastic antiquarianism, and little science. A depressing amount of entomological taxonomy, especially in Europe, consists of long and lengthy discussions of this type of taxonomic book-keeping (to avoid this, some of the best taxonomists I know work only in the tropics where they can be biologists rather than archivists). For Frank, pursuing this did not seem a great career move for a recently graduated student; in fact, the choice wasn’t there — no one would fund it. We never submitted a grant, but I did ask a senior science funding figure what would have happened if we did. His answer was clear — “why should we spend science money on a project that will be 90% book keeping and result in a technical publication in an obscure journal that will not be used by anyone except other taxonomists and which will be out of date in a decade”. Perhaps this overstates the case, but it is hard to argue that it is good value for money. I do not think the Alloxystinae will ever be revised as things stand at the moment.

It is dangerous to draw too wide conclusions from a single group (or, depending on your viewpoint, from what one critical reviewer called an unsubstantiated diatribe), though the Alloxystinae are far from unique in their intractability. But I derive two main lessons from this experience. First, the way we do taxonomy now, as encapsulated in the Zoological and Botanical Codes, may be part of the problem with attracting new funds to the field. The Linnaean system and the Codes have done a fabulous job in stabilizing nomenclature and have created a classification of the living world that is one of the triumphs of modern science. But these mechanisms were honed in an age of paper and post, and makes poor use of modern information technology. As I shall argue below it can be done better today, and the transition to something better can be carried out in a way that preserves the best of 250 years of Linnaean taxonomy but which jettisons some of the accreted historical baggage. Second, if taxonomy does not change to make it more relevant to the way that science is done now it will be replaced. Our modest use of molecular techniques helped immeasurably to sort out difficult issues in the Alloxystinae and the coming couple of decades will see radical advances in the speed, cheapness and accessibility of DNA sequencing. I think that there is a real possibility that massive parallel sequencing of genes from huge numbers of individuals will be able to create a classification from scratch. Whether this replaces or meshes with the Linnaean system depends on how the field evolves in the next ten years or so.

UNITARY TAXONOMIES

One of the difficult things today for consumers of systematics is the distributed nature of the taxonomy. By this I mean that the taxonomy of any particular group does not exist in a single location but is an ill-defined integral of all the papers, books and monographs on the taxon, backed up by types in museums and herbaria. To be an expert in a group is as much to know the topography of this information landscape as it is to be able to identify different organisms, recognize new

species, and determine their phylogenetic relationships. The complexity of this information excludes the majority of non-specialists from the subject, with two consequences. First, they can only use taxonomic resources when higher-level works such as accessible monographs, floras and field guides are available (and are reasonably up-to-date). For huge stretches of the animal and plant kingdoms they are absent. Second, the work of taxonomists impinges little on the daily lives of other biologists, who thus insufficiently appreciate its importance.

Another difficulty for the non-specialist is divergent taxonomic opinion. In many groups there are competing views about how best to classify different taxa, and for some — groups of cacti, orchids and butterflies, for example — this can be a nightmare. When faced by criticisms from other biologists about this lack of consensus taxonomists often reply by pointing out, rightly, that every taxonomic scheme is a provisional hypothesis, and that the presence of alternative concepts is part of the healthy sorting out of ideas that occurs in all the sciences. Indeed, it is proof, if proof is needed, that taxonomy is a vibrant science and the discord and discourse should be encouraged. Criticisms of this type are sometimes characterized as naïve and stemming from a simplistic and old-fashioned view of taxonomy.

I fear that taxonomists who respond in this manner underestimate and in some cases patronize their critics. Most people who use taxonomies understand their provisional nature, and accept that they will change as knowledge accumulates (though they also tear their hair out when a name changes purely because some archaeological research in a museum has reinterpreted an overlooked type or discovered an early description). But I think it is perfectly reasonable to ask at any one time for a provisional consensus treatment that can be used consistently by consumers. This sometimes exists *de facto*, where there is a single authoritative revision or monograph, but the Codes have no mechanism for supplying a consensus, and give no guidance as to how the end-user should treat radically different taxonomic opinions.

My view is that for taxonomy to be better appreciated and better funded it must address the issues of its distributed nature, its lack of consensus, and elements of its historic baggage. It must do this in an evolutionary manner that preserves the best of its immense achievements. I am sure there are different ways this could be accomplished, but here I am going to discuss one idea which I have called “unitary taxonomy” (Godfray 2002a). I make no pretence that is the optimal or even a good candidate solution, but I hope that discussing its multiple failings might suggest a better way of proceeding.

My argument is that we need to move from the distributed taxonomies of today, only fully usable by those with access to large, specialized libraries, to unitary taxonomies fully accessible on the web. By unitary taxonomies I mean a systematic treatment of a significant taxonomic group of organisms at a global scale that includes the taxa descriptions and diagnoses that one finds in traditional taxonomic works, supplemented where necessary by all the kinds of information resources that the web can provide. The unitary taxonomy site would be a “one-stop shop” for taxonomic information on that group, and would contain both the current consensus taxonomy for the user community, as well as alternative hypotheses for future research by the taxonomic community.

How might this work in practice and, in particular, how would the initial transition from a distributed taxonomy to the “first web revision” occur? Let us suppose that one of our great museums offered to host the unitary taxonomy of the Culicidae, the mosquitoes — a group whose taxonomy is both difficult and of immense importance in disease control (I shall return later to issues of determining who should host what revision). The museum would then set up a committee to co-ordinate the preparation of the first web revision, the group acting rather like the editorial board of a scientific journal. The revision would consist of separate “pages” for each taxon — species, genus, etc. — which at the minimum would contain the information required for a current species or higher

category description. That is, a full description with the designation of a type specimen. An advantage over the current system is that the committee would almost certainly want to set a standard for descriptions so that information on certain characters is consistently available across all groups. One could envisage character matrices being automatically constructed, though other information would also be included. Mosquitoes, like other groups, have a large excess of names over valid species and the first web revision would also need to include "pages" for these synonyms, etc. linked to valid taxa. As this information accumulates for different genera, tribes and subfamilies it would be mounted on the web and offered for web-based, public refereeing by the mosquito-systematics community. The process of refereeing would be handled by the taxon committee who would determine the consensus taxonomy that would become the first web revision. Critically important though, the process of deciding on a consensus should not exclude divergent views. Any alternative hypothesis should by right be mounted on the unitary taxonomy site where it will be available for research and discussion and possible incorporation into a future revision.

How would taxonomy proceed after the transition to the web? Most importantly, the first web revision would determine the set of names and taxa that need to be considered in any future research. If I think I have found a new species I need only consider the taxa (and names) on the first web revision in deciding whether it is actually undescribed. At a stroke, much of the sterile part of modern taxonomy is dispensed with — the unprofitable searching through old literature and collections. After the first web revision, the complete relevant literature for the group will be at a single site. For sure, consultation of types will continue, though increasingly high quality photographs, produced by systems with perfect depth of focus, will be mounted on the web and actually be easier to use than the original specimen.¹ Suppose a new species is described on the web and then subsequently a 19th century description is unearthed. At present, the old name would take precedence (or would need to be formally suppressed), but in this system it would have no status beyond that of a historical footnote that might be included on the species web page.

Taxonomy does not stand still and new research will require changes to the first web revision. I envisage new species and revisions being mounted on the web for public comment and refereeing, and then periodically a new consensus "current web revision", arbitrated by the taxon committee, being "published" (with rejected hypotheses still being available). This would replace but be linked to the previous set of revisions. A great advantage of web-based taxonomies is that species concepts can be followed both backwards and forwards through time. Thus, suppose that I, a non-taxonomist, publish a paper in which I refer to a particular species of mosquito. Today I might give its Linnaean binomial and author but were there a unitary taxonomy I would refer to its URL (or more likely a more sophisticated form of digital object identifier, DOI). The reference would link specifically to a taxon and revision edition. If in the future the species concept or taxonomic context changes then I can use the DOI to trace forward through time to discover what name people are currently referring to this species by. Similarly, given a species of interest it would be possible to go back through time to pick up references to it by whatever it used to be called. Today journals tend to be rather unclear and lax about how they demand species names to be referred to, while normally being very clear that references to DNA sequences, for example, have a database reference. A unitary taxonomy would provide a simple and valuable means of clarifying what the author means when he or she uses a binomial, while incidentally reinforcing the continuing relevance of taxonomy for the whole biology community.

Web revisions, as I have just described them, are essentially taxonomy as currently practiced.

¹ A unitary taxonomy could operate perfectly well with the current system of holotypes, paratypes, lectotypes, etc. I suspect that increasingly there will be a movement to choose new replacement modern types that are both fresh and undamaged for image capture and DNA archiving.

but placed within a modern digital information framework, and with the novel addition of the consensus taxonomy. Once such a unitary taxonomy had been set up, it could be extended very easily to provide much greater information resources. The most obvious extension is to provide more space for descriptions. Taxonomic works are often famously difficult to use, employing a recondite vocabulary, impenetrable to the non-specialist. Part of the difficulty is the genuine subtlety of species distinctions and the requirement for expertise in the group before safe diagnosis is possible. But much of the difficulty also stems from the requirement, imposed by the economics of publishing, for taxonomists to be brief, even telegraphic, and to use a minimum of expensive illustrations (ideally not in color). The marginal costs of extra storage on web servers is minimal and this will give taxonomists the space they need to be understood.

Descriptions are not the only information about a species that would be included on its web page. It will of course be straightforward to link to phylogeny projects, for example the "Tree of Life" initiative <<http://tolweb.org/tree/phylogeny.html>>. Many other sorts of data might be mounted there, and further resources might be accessed through links. Returning to our mosquito example, almost certainly one would want to accumulate information about early stages — eggs, larvae, and pupae — all of which are important for vector biologists. Cytology, and increasingly molecular biology, have played major roles in mosquito taxonomy, and for critical groups there would be illustrations of polytene chromosomes with inversion patterns, and sequence information for relevant loci. While the first web revision might just give fairly general information about geographic distribution, as museum collections are digitized and linked to GIS information one could easily imagine more sophisticated treatments of distribution emerging with unitary taxonomy web sites interrogating museum sites that link to them and automatically generating maps of known distributions. As authors elect (and journals require) species names to be linked to the web site then the unitary taxonomy will become ever more useful in accessing the primary literature concerning different taxa. Increasingly, taxonomists and the institutes they work for would move from being curators of specimens to curators of the body of information about their chosen groups.

The raw descriptions and associated data are of value to taxonomists and, to a more limited extent, other biologists, but to be maximally useful a unitary taxonomy site would need higher-level treatments of these basic data. A simple step would be to allow the selection of taxa from restricted geographic distributions so that to identify a mosquito from my garden in England I would not have to wade through Australian and African species. But the web site should also attract more sophisticated identification tools such as traditional and multi-access keys that can make use of the library of visual images stored at the site, and include as well the type of information that can be found in regional floras and field guides. Such resources would be directed at both the professional and amateur biologist, and at a yet higher level of abstraction one might want to encourage applications aimed at a very general audience: to enable a member of the public to work out the mosquito biting him or her on their porch, or to identify the pretty moth at the light. The ultimate aim would be to have a democratized site that anyone could enter at the appropriate level, and once in could then delve as deeply as they required. Apart from its obvious usefulness, such a site would again reinforce the contemporary relevance and importance of taxonomy.

What are the downsides of unitary taxonomies (Knapp et al. 2002; Thiele and Yeates 2002; Scoble 2004)? Critics have accused it of being authoritarian and at variance with the *laissez faire* traditions of taxonomy. I hope the arguments above dispel some of these concerns, in particular the worry that alternative views might be excluded by a taxonomic clique. But it is true that one particular set of hypotheses will be designated the current consensus taxonomy. I argue that the increased engagement with the user community is a price worth paying for this extra burden (Godfray 2002b).

To my mind, a much more serious concern is the costs of maintaining and curating a unitary taxonomy web site. There are hardware costs in setting up the site, but probably more important are the salary costs of its maintenance. An advantage of the current system is that if no one is interested in the taxonomy of a particular group it can quietly snooze in the library; a unitary taxonomy is harder to put on one side. I believe that the task of creating and maintaining unitary taxonomies should be taken on by our major museums and herbaria, all of whom, virtually without exception, have enthusiastically embraced the web. It is a natural extension of many of their current activities. But, indubitably, for them to do it would require new funds.

Were unitary taxonomies (or a related idea) thought to be worth pursuing then the only sensible way of proceeding would be to experiment with one or a few taxa, perhaps of the size of the Culicidae. If the project failed, or the resulting resource was judged poor value for money, then no bridges are burnt and the original distributed mode of taxonomy can easily be re-adopted. But my hope is that the clear benefits of the unitary site would leverage the new monies for taxonomy that would be required to extend the project. I think it would generate the constituency that would support and militate for more taxonomy. Converting all of taxonomy to the web will take a very long time, but during this period both the current and unitary models can co-exist for different groups.

There are a series of other issues that would need to be overcome. Some body, the equivalent of those administering the Zoological and Botanical Codes, would need to approve an application from an organisation to mount a unitary taxonomy, and to ensure they have an appropriate taxon committee, long-term commitment, etc. To a certain extent this would be self-policing as a site would only be declared a unitary taxonomy after it had produced the necessary resources, but the central body would probably need to give the final approval. Another issue that is often raised is the problem of backup and ensuring that the information is not lost. While a real concern, I believe it easily dealt with; there are not hard copies of many of the genome-scale data bases of molecular biology.

A further criticism is that unitary taxonomies are elitist because they require access to the web. I think this is daft; distributed taxonomies are extraordinarily difficult to get hold of. Even if you can list all the relevant papers and books, they are frequently in obscure journals or very expensive monographs. Few people have easy access to the small number of taxonomy libraries that have a reasonably complete coverage of the literature, and, for those who don't, assembling the resources to do taxonomy is difficult and costly. A unitary taxonomy web site should be open access to everyone, and in my view should also be downloadable so that it can be used in the field where internet access is impossible. And as a final option, all or part of it can be printed out.

A more serious criticism is that of language. I think taxonomy is a science and today, inescapably, the *lingua franca* of science is English — unitary taxonomies, at least the taxon pages, should be in English and replace the current polyglot distributed model. At its worst, this means taxonomists learning one extra language instead of the several they typically require now (though as a monoglot English speaker I feel decidedly uncomfortable in advancing this argument). But, though the basic data would be in English, there is no reason why the higher-level components, the keys and material aimed at the general public, should not be in whatever language or languages are most appropriate.

Having discussed the costs of adopting unitary taxonomies, I want to finish this section by arguing that there are serious costs for maintaining the *status quo*. The first of these I have already alluded to: Taxonomy is failing to generate enough products that are of value to its end users, and many are, at best, indifferent to taxonomy and are failing to argue for new monies going to the subject. I believe that unless taxonomy produces resources that are valued by the rest of biology it will wither on the vine.

An optimist might counter this argument by saying that we will always need a system of classification and hence that, imperfect as it is, taxonomy as currently practiced will muddle along, very much as it has over recent decades. Why tinker with something that works? But there is an alternative to Linnaean taxonomy looming on the not too distant horizon. The speed, efficiency and cheapness of DNA sequencing has steadily increased over the last two decades at a rate that shows no sign of declining. Already there are arguments that much species-level identification can be automated and done by sequencing: the DNA bar-coding and related initiatives (Hebert et al. 2003, 2004; Stoeckle 2003). At the moment, routine sequencing to identify individual specimens is normally not cost effective but this will almost certainly change in the coming years, and it is not a complete flight of fancy to imagine a future when species identifications can be done routinely by machines in the field (Janzen 2004): the tricorder solution (recall the useful gadget in the *Star Trek* program). Ideally, this new technology will interdigitate seamlessly with current Linnaean-based methods, and if unitary taxonomies are adopted this will be particularly easy. I worry that if taxonomy continues as it is, in its current complex, distributed mode, then it will not mesh with DNA-based methods and be replaced by them. It will be easier for many groups to start from scratch and define species and higher taxa as clumps in sequence space than to try to relate them to the existing system. Would this matter? I think it would. We would throw much of the biological knowledge that we have accumulated over the last 250 years, a large amount of which we would have to discover anew. And we would also divorce sequence-based identification from the more traditional methods based on morphology, that will ensure continue, at least among the amateur consumers of taxonomy.

A final point: there are already a wide variety of interesting and important taxonomic resources on the web, though none I believe approaching a unitary taxonomy website as I have described here. To explore these sites a good point of entry is the Global Biodiversity Information Facility (GBIF) portal, <<http://www.gbif.org/>>.

NEW RANK-FREE TAXONOMIES

While unitary taxonomies seem revolutionary to some they are tame compared with some of the other alternatives to Linnaean taxonomy that are being advocated at the moment. Perhaps the most radical is the replacement of Linnaean binomials and taxonomic hierarchy with a rank-free system based purely on phylogenetic principles and regulated by a new set of naming rules, termed the PhyloCode <<http://www.phylocode.org>>. The logic behind this is to acknowledge the arbitrary nature of taxonomic ranks (including, depending on your point of view, species) and to incorporate rigorous phylogenetic definitions of different taxa. While acknowledging the arbitrary component of assigning ranks, and the importance of rigorous phylogenetic methodology, my view is that switching to such a system would be an unmitigated disaster that would risk the destruction of taxonomy.

Taxonomists are often unfairly caricatured as inward-looking and obsessed with changing names for reasons that have little to do with biology, and a lot to do with the formal rules of systematics. Such a wholesale revision of names as the PhyloCode envisages would confirm all the worst prejudices that outsiders have about the subject and would probably destroy its funding base. There are also technical objections to the PhyloCode (see, e.g., Forey 2002; Wheeler 2004) concerned with the instability of nomenclature as evolutionary relationships are resolved or new taxa are discovered that render old ones paraphyletic. In addition, an extremely important gift of the Linnaean system to the rest of biology is a hierarchical series of partitions of biodiversity, however imperfect that might be. An ecologist can work with the generic and family diversity of organ-

isms at one field site, and compare it with that at another. He or she knows that taxon distinctions are arbitrary, but this is relatively unimportant in comparative studies using the same taxa. Similarly, information can be organized at different levels; keys exist to the families of flowering plants, and many major garden plant encyclopedias are arranged as alphabetical lists of genera. Were taxonomists to abandon ranked taxa, they would be re-invented by ecologists, naturalists and gardeners. I suspect that there will continue to be a need for hierarchical partitions and their provision is best left to taxonomists. These all seem to me compelling arguments against kicking over the traces and abandoning the Linnaean system for something untried and with questionable general support. And from a phylogenetic perspective what matters is tree topology rather than the naming of nodes: it is not as if we cannot have our cake and eat it too. Linnaean taxonomies can be linked with phylogenetic hierarchies so that you have the benefits of both. Perhaps unsurprisingly, I would argue this is another benefit of a unitary taxonomy.

CONCLUSIONS

For taxonomy to survive and prosper in the 21st century it needs to identify better its end users and its functions. For the taxonomy of living plants and animals, with which I have been most concerned here, the ultimate function of much of taxonomy is to enable further research in whole-organism biology, and of itself to produce a classification of the world's biodiversity with an account of their interrelationships and the tools required for their identification. There are major constituencies to support investment in both functions. The first constituency is other whole-organism biologists and possibly biologists in general. The second constituency is potentially everyone, from professional biologists to anyone who has ever wondered about the name or natural of a particular plant and animal. There should be a chorus clamoring for more taxonomy, with a much broader base than the relatively narrow interest groups that are currently arguing for greater funds. I have no illusions that unitary taxonomies as I have described them are the solution to these problems, but I do believe that some much better idea, that would convert the current distributed mode of taxonomy to a one-site form that is much more easier to use by the community, will be at least part of the answer.

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Naming the World: Is There Anything Left of Linnaeus?

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Linnean Taxonomy has been ripped from its philosophical foundations, plastered with additional conventions and moulded to serve a variety of functions. Little remains of its original formulation and even that which does has been criticized for being unsuitable for classifying an evolving biota. The chief target for attack is the Linnean rank (Genus, Family, Order etc.). Here, I argue that, while most ranks cannot be defended, the genus and species should be retained as the binomial. This is for practical reasons. Genera are recognized by discrete characters whereas species rarely are. Different workers have very different ideas of species, both theoretically and in recognition criteria. In naming the world our efforts will be more fully rewarded if we concentrate on compiling lists of genera as a proxy for biodiversity estimates.

Carl Linnaeus (1707–1778) laid the foundations of our current systems of taxonomy which are now administered through the various international codes of nomenclature. Nowadays, we accept that it is a system much modified from that which he set up, and some (de Queiroz 1992; Ereshevsky 2001) would say it has outlived its usefulness and deserves to be replaced. So, in answering this question posed by the above title most people would probably agree that the only thing left of Linnaeus is his skeleton, lying beneath an inscribed slab in Uppsala Cathedral.

We no longer share Linnaeus' belief that all of biodiversity was specially created on an island called Paradise, located somewhere in the Indian Ocean. We no longer believe that there is a fixed number of animals and plants. We no longer believe that order in the natural world can be reflected using essentialism and the principles of logical subdivision, and we question many of Linnaeus' practical methods for classifying life, especially the use of ranks (Class, Order, Family, etc.) and the monothetic recognition of groups (groups recognized on the variation of a single feature). Yet, I suggest that there are some elements of the system of taxonomy and nomenclature started by Linnaeus (here called Linnean Taxonomy) that we need to maintain in order to provide effective communication about relationships between organisms, to meaningfully discuss patterns of biodiversity, and in order to be effective in bringing our taxonomic conclusions to as wide an audience as possible. I use the phrase Linnean Taxonomy, rather than refer directly to Linnaeus because many aspects of Linnean Taxonomy are modifications of those proposed by Linnaeus himself.

LINNAEUS' ACHIEVEMENTS

In our modern world, imbued with very different belief values from those of Linnaeus' day, it is all too easy to lose sight of his achievements and the progress he made relative to what had gone on before him. It may be instructive to review briefly what Linnaeus set up for us in the first place and why. Prior to Linnaeus' work in the 18th century, the names of animals and plants were not fixed. Often the actual name applied was effectively a short description, encapsulating the observ-

able features of the organism. For example, a species of bindweed, *Convolvulus*, was named *Convolvulus folio Althae* by Clusius in 1576. In 1623, Bauhin named it *Convolvulus argenteus Althae folio*. And Linnaeus named it *Convolvulus foliis ovatis divisis basi truncatus: laciniis intermedius duplo longioribus* in 1738 (Stearn 1971:247).

Linnaeus recognized the potential confusion that could arise by giving different descriptions to the same kind of organism, and he gave us guidance in three main areas:

- (1) He provided some rules for sorting organisms into taxa.
- (2) He established some rules for naming those taxa.
- (3) He provided us with a hierarchy of ranks, or categories by which taxa could be grouped into increasingly more inclusive sets: Variety, Species, Genus, Order and Class (we use many more ranks today).

His rules for sorting taxa were those of Aristotelian logic of subdivision that employs the concept of *genus* and *species*. The *genus* has a recognizable essence: that is, a property or properties "that makes it the type of entity that it is" (Ereshevsky 2001:17). As a subdivision of the *genus* there are the *species* variations on the essence of the *genus* recognized by differentiae. The word *genus* here is used in a philosophical sense but Linnaeus co-opted it for use as one of the many ranks in the Linnean system.

Linnaeus recognized that the essence of a plant allows the plant to breed true. For Linnaeus, the *genus* was the crucial entity. He believed that the essence of the *genus* lay in the fructification (the flowers and fruits). It was the variation in the parts of the flower and fruit that allowed us to discover the essence. Figure 1 shows his descriptions of the essences of two genera of Rannunculaceae (buttercups and their allies), where it can be seen that these are combinations of features of the calyx, corolla, stamens, pistil, perianth and the seed. The descriptions of the essences are equivalent to one another; that is, there are descriptions of the same six parts of the fructification. There was for Linnaeus the notion that one *genus* of plants was equivalent to another.

The species of genera are recognized by the differentia — variations on the generic essence. He used features of the leaves, stems, roots, etc., as descriptors of such variation. For instance, when diagnosing two species of plantain (genus *Plantago*) he named one "*plantain with pubescent ovate-lanceolate leaves, a cylindric spike and a terete scape*" and distinguished from "*plantain*

Thalictrum

CALYX: nullus

COROLLA: petala quator, subrotunda, obtusa, concava, caduca

STAMENS: *Filamenta* plurima, superne latiora, compressa, corolla longiora, *antherae* oblongae, didymae.

PISTIL: *Styli* plurima, brevissima. *Germina* singulis stylis solitaria, subrotunda. Stigmata crassiscula

PERIANTH: *Cortex* sulcatus, carinatus, unilocularis, non discedens

SEED: solitaris, sublonga

Trollius

CALYX: nullus

COROLLA: petala quatuordecim circiter, subovata, coniventia, decidua; in seriebus exterioribus tribus terna; in intima feriequina

STAMENS: *Filamenta* numerosa, setacea, corolla breviora, *antherae* erectae.

PISTIL: *Germina* numerosa, sessilia, columnaria. *Styli* nulli. Stigmata mucronata, staminibus breviora

PERIANTH: *Capsule* numerosa, in capitum collectae, ovate, acumine recurvo

SEED: solitaria

FIGURE 1. Generic essences for two genera of Rannunculaceae as spelled out by Linnaeus. Note there are descriptions of the same parts of the fructification in both.

with lanceolate leaves, an almost ovate naked spike and angled scape" (I have taken this example from that given by Stearn 1971). These were the distinguishing features of the species within the genus *Plantago* that had already been recognized and described by its essence. But a species could not stand by itself. You could not call something "lanceolate leaves, an almost ovate naked spike and angled scape." The diagnostic attributes had to be linked with a genus name. Therefore, there were always two parts to a biological species name — the genus, with its essence, and the species, with its differentia. Like the genus, Linnaeus regarded one species as equivalent to another.

Quite a lot has been written (see Härlin and Sundberg 1998 for discussion) about how a name that we give to something is quite separate from the description of that entity — or how we recognize it. This was not so for Linnaeus and, in practical terms, this does not seem to be the case in day-to-day taxonomic practice. When, we speak of *Rannunculus repens* or *Clupea harengus* we imply certain morphological attributes: characters that we have learned and identify with the name. Modern formal nomenclature still retains this association between the name and characters in two ways. First, the nomenclatural codes insist that there is a description with a name of a species. If not, the name is a *nomen nudum* — a name without a description — and is invalid. Additionally, if the description is ambiguous or too general to be of any diagnostic use it is a *nomen dubium* and similarly is invalid. Secondly, we insist on an actual specimen — a type specimen which must be there to be consulted at any time to check to see what the original author was describing. The insistence of the type specimen was not Linnaeus' idea. That came much later (Strickland et al. 1843 for zoology and Arthur et al. 1904 for botany). Despite being bolted on to Linnaeus' original method, it is this link between a name and characters through the intermediary of the type specimen that remains of Linnean Taxonomy.

There are other reasons why maintenance of the binomial may be advantageous. Linnaeus was a very practical person who realized that it would be impossible for people to remember all the long descriptions of genera and species, so he shortened them to two — the binomial — which, by convention is italicised to distinguish it from all other Linnean ranks. But in shortening the name he did not expect the descriptions to be dropped. He also realized that it would be impossible for anyone to remember all the species names (for example, about 8000 species of plants were known to Linnaeus), but he considered that it was well within capabilities to remember 300 generic names. Furthermore, current generic diagnoses — while they are based on a completely different theoretical footing than those of Linnaeus — tend to be relatively clear cut with presence/absence features most often used. This contrasts with the species diagnoses which are, more usually than not, combinations of morphometric variables (length/breadth, patterns of color, counts of parts). These are far more difficult to commit to memory, as well as being susceptible to the sample available at hand when the species is named. Combining the generic and species names allows a much more complete, manageable and accurate description to be implied by the name. Even today, it is perfectly possible to remember generic names and their meaning, although such practice is limited to much smaller taxonomic groups than "plants" or "animals".

Another reason for maintaining the binomial is that it does give us some indication of the relationships of that species. This is because a Linnean binomial, such as *Clupea harengus*, tells you something about relationships. In other words, it implies a taxonomic address. It tells you that species *harengus* (Atlantic herring) is in the genus *Clupea* and therefore is probably more closely related to the species *pallasi* (Pacific herring) — which is also in the genus *Clupea*, than it is to species in the genus *Salmo*. There is a downside to this. If our ideas of relationships change, then so must the name. And an investigator may be forced to place it in a genus even if the relationships are uncertain, or create a new genus, only because of the demands of the Linnean system (Cantino et al. 1999).

A final reason why the maintenance of the binomial is advantageous is that species names, used by themselves as uninomials, might lead to confusion. Many species epithets are the same, even though they are used for very different animals and plants. For instance, if we just used a specific epithet to refer to a species, such as *vulgaris* (meaning common), or *sylvaticus* (meaning inhabitant of woodlands) or *borealis* (inhabitant of the Boreal Region), we would have to employ some other convention, such as the attachment of a number (e.g., *vulgaris*623) to be clear to which species the name referred. Such has been suggested by those who would like to move towards unino-mial names for species (Cantino et al. 1999).

Linnaeus made a logical break between the genus and more inclusive categories (see below). For Linnaeus, the species was nothing special — it was just a variation on the genus essence. Today, species are regarded as the engine of evolution, and if we make a break at all (and not every-one does) it is at the species level. Readers should be aware that there is split in the taxonomic community between those who consider that the species is just like any other rank and should, therefore, be considered and named in the same way (for discussion, see Mishler 1999) and those who consider that the historical connectedness between members of species (individuals) is different from that “connecting” species in genera (Rieppel 1988).

Although Linnaeus was certain that his ranks of Genus and Species were natural (in his terms), he was less certain about the naturalness of the ranks above the level of genus. He used two other ranks, Classes and Orders, which we still use today. However, he claimed that his system of recognizing Orders and Classes was artificial because he differentiated his Orders from one another and Classes from one another on single — not on the combinations of — characters that he had used for his genera and species. That is, his Classes and Orders were monothetic divisions (i.e., based on variations in a single character). For instance, his Classes were distinguished from one another on the numbers and positions of the stamens. As long as the stamens were there the number and position seemed of no biological or vital importance for the maintenance of the genera and species (that is, they were not *essential*). He recognized that such variation, expressed through his recognition of Classes, may be useful to segregate plants into groups as an *aide memoire* even though there was no implied naturalness.

It is also worth emphasising that Linnaeus thought that he had all of the biological universe before him. There were no undiscovered species (although he did acknowledge limited speciation through hybridization), and we had all we need to know in front of us. It was just a case of subdividing that which was on the table — and that was it. Nowadays, of course, we recognize that we do not have the universe; neither, the total number of species nor total knowledge of the variation of those species which we have recognized. This is why our classifications must change, to incorporate new knowledge. So the credo that classifications need to be stable either in content or naming seems an unreasonable expectation. The trick, of course, is to devise systems of classification and naming that will be least perturbed by newly discovered taxa or relationships. Unfortunately, Linnaeus’ system, which we have inherited and modified, is particularly bad at this. And this is because of his insistence on rank.

Any newly discovered taxon or newly investigated character complex (for instance molecules) can change our ideas of relationships among taxa. As a paleontologist I am particularly affected by this. Fossils tend to come with particularly unexpected combinations of characters that, more often than not, tend to place them as plesiomorphic taxa to extant sister groups. If we wish to indicate the relationships among the taxa in a written classification, some accommodation is necessary. This is best illustrated by example which I take from Forey et al. (2004). Consider the phylogeny of a group of Recent teleost fishes (Fig. 2A) with a standard ranked classification immediately to the right of it (3C). We may wish to introduce two fossil taxa and write the classification to indicate

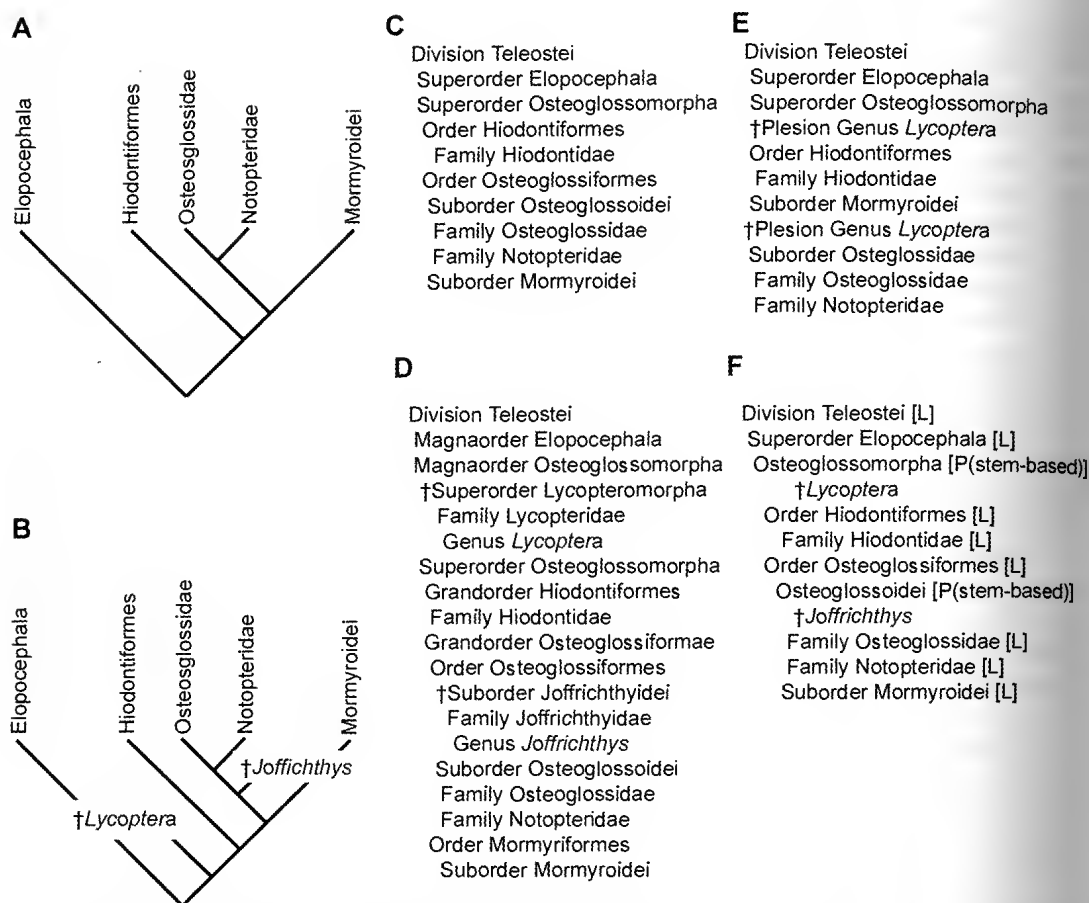


FIGURE 2. Introduction of additional taxa — in this case two fossils — can cause problems for ranked nomenclature. There have been various solutions to this problem, some of which are shown here (see text for discussion).

their relationships. The phylogenetic position of the fossils (†*Lycoptera* and †*Joffrichthys*) are shown in Figure 2B (Note: these could just as easily be Recent taxa but fossils are chosen here to illustrate one of the alternative solutions that caters specifically for fossils). We have a number of alternatives by which we could write a classification to express the phylogeny, only some of which are shown here. We could simply increase the number of ranks as shown in Figure 2D. This has two deleterious effects. It demands that we make new and perhaps unfamiliar intermediate ranks (for example, introducing the ranks Grandorder and Magnaorder, in which I have followed McKenna (1975) who used these in a “real” classification of mammals). It also demands that we change the rank of existing names. For example, the Superorder Elopocephala in the original classification now becomes a Magnaorder Elopocephala. This may also have the unfortunate consequence in demanding a change in the name ending, because the international nomenclatural codes have recommendations for the endings of certain ranks. In addition, different authors may decide to play the rank game in different ways because there are no rules as to what ranks to use beyond the fact that the zoological and botanical Codes demand that species be assigned to ranks up to and including the family.

Other suggestions ignore the rank. There are two shown here. One is called the annotated

Linnean system (Fig. 2E) (Wiley 1979). This uses a sequencing convention in combination with the rankless modifier “plesion.” Here the Recent taxa are listed according to their branching order without indentation. The Recent ranks are retained to provide a link with previous classifications but they have no specific meaning here. The fossils are introduced as a Plesion. Plesion (literally — plesiomorphic sister-taxon) can be associated with any Linnean rank (Order, Family, Genus, Species, etc.) and simply means that it is to be considered as the extinct primitive sister-taxon to the taxon listed below. In other words, the rank of the fossil group Plesion is decoupled from that of the rest of the hierarchy.

A third way (Fig. 2F) is to deliberately abandon Linnean rank and construct names with a specific phylogenetic definition tied to a particular phylogenetic hypothesis. This last is the method suggested by the PhyloCode (Cantino and de Queiroz 2000). Here we have to discriminate between a name to be used in a Linnean sense and that in a PhyloCode sense. That is why, following PhyloCode recommendations, the suffixes [L] and [P] are inserted behind two of the names and the Linnean rank is removed. Furthermore, under PhyloCode we have to stipulate in what sense the particular PhyloCode name has been established. In this case, the stem-based definition of a clade has been chosen, but this is one of many phylogenetic definitions of a name that may be employed.

There are other ways, exemplified by the rank-free classifications of land plants as established by Crane and Kenrick (1997) where there are just names and the indentation on the page of the written classification indicates the shape of the phylogenetic tree. There are also numbering systems where clades are numbered according to an hierarchical fashion (Hennig 1966; Løvtrup 1977) which are perfectly logical but difficult for a biological culture that has grown up with word-based taxonomy to absorb (e.g., Clupeidae may be known as 6.4.5.1.2.3).

Thus, there are many good reasons to agree with the calls to ignore rank. But I say ignore rather than abandon because there are many people who maintain that rank does help them in their everyday work, and I would agree with this latter group up to the genus. As a paleontologist, I cannot ignore the multitudinous graphs and tables showing plots of the diversity of organisms through time. Most of these are compiled from data gathered at the Linnean generic and family levels. But this is a practical necessity of using the genus and maybe the family as a proxy for species durations, rather than a conscious effort to target genera and families.

No matter whether a genus or family is used, it is imperative that the status of that group is given by the author. The PhyloCode insists that only monophyletic groups be named. No one would disagree with the desirability of monophyletic groups. However, it is unrealistic to expect the PhyloCode to be capable of naming but a small percentage of life. It is much more practical to include all taxa that you may wish to name, with or without rank, but to identify them as monophyletic, paraphyletic and polyphyletic groups, or even status unknown. It would then be up to the consumer to decide whether certain named groups are going to be useful for his or her purpose. A great deal of the confusion surrounding the calculation of diversity curves is caused by not knowing the phylogenetic status of the taxa listed in the various data bases (see Smith and Patterson 1988 for a good example).

Therefore, I would agree that we have abandoned all of Linnaeus' theoretical underpinning. Despite this, and despite all the modifications to Linnaeus' original system of taxonomy and nomenclature, we have retained the binomial and the link with characters through type specimens. I do not find this surprising because the advantage of the Linnean system is that it is basically agnostic to any causal explanation we may invoke to explain diversity.

FUTURE OF TAXONOMY

So what about the future of taxonomy? I would like to address this in the field I know best — paleontology. For this I would like to draw information from Forey et al. (2004). In this paper we first asked ourselves how good we were, as a paleontological community, at documenting the fossil record.

There are at least two aspects to “how good”. How well have we sampled the fossil record and how good are we at documenting it. In terms of sampling paleontologists have done well. Given the constraints of fossilizable parts of animals and plants (probably about 5–10% of all organisms that have ever lived entered the fossil record, Paul 1998). Given the constraints that some paleoenvironments will be preserved (near shore marine environments) and some will not (e.g., high montane regions), and given the constraint that only a fraction of the rock record survives today — it as has been estimated that more than 50% of the species in rocks available at outcrop are now documented. If we add the fossilizable component to that which has been lost due to the attrition of the rock record through erosion, subduction, etc., then probably 1–5% of the biota is preserved as collectable fossils. Low as this may seem, we do seem to be getting better at documenting the record we have. Paul (1998) looked at the proportion of new species in monographs throughout the latter half of the 20th century that represented genuinely new finds, as opposed to reinterpretation of earlier collected material and concluded that only about 40% of the newly erected species were the result of new collections. Sixty percent (60%) were discovered as the result of revision.

How good are we at documenting the fossil record? It turns out again that paleontologists are quite good — at least superficially. This is probably because paleontologists have a long history of documentation as part of their everyday work and the fact that many fossils are used for stratigraphic and commercial purposes encourages this.

Table I lists some of the major compendia for fossil groups, and without going into detail most of the fossilizable animal and plant groups are covered. However, a number of comments are in order. Virtually none are web-based and/or updated on a regular basis. If they are updated it is more usual for wholesale revisions to replace earlier attempts than for constant updating. Since most are hard copy or even CD Rom-based, then any information is always immediately out of date. Most often wholesale revisions are done by authors different from the original or preceding author(s). Because of this, there can be very different concepts of species and genera, and especially very different ideas of higher classification leading to very little continuity between revisions.

This last point is best illustrated by example from the field of fossil fishes, although other people can substitute their own case histories. In the history of paleoichthyology there have been only two people who were in a position to fully appreciate the total diversity: Louis Agassiz who wrote *Les Poisson Fossiles* between the years 1833–1844, and Arthur Smith Woodward, who wrote the *Catalogue of Fossil Fishes* between the years 1889–1901. These two people in their own eras saw at first-hand all, or nearly all, the specimens of fossil fishes that were in existence. Agassiz and Woodward saw the same specimens. Woodward, of course, saw many more collected in the heyday of the Victorian accumulation which separated these two works. Therefore, like Linnaeus and his plants, Agassiz and Woodward each had the contemporaneous universe of fossil fishes before them. All they had to do was to divide that universe.

Agassiz divided his fishes into four groups characterized by their scales — placoids, ganoids, cycloids and ctenoids. He recognized a total of 1223 species in 348 genera, an average of 3.5 species per genus, split into the systematic groupings as shown here (Table 2). Woodward recognized 1167 species in 391 genera, an average of three species per genus. The numbers are comparable. If we look at just two of these groups the comparison becomes even closer. Agassiz' cycloids

TABLE 1. This table lists some of the major data-bases, compendia and lists of fossils with some indication of their information content. From Forey, *et al.* (2004) where further annotation of this table is given.

Group	Most exclusive taxonomic level	Diagnosis most exclusive level	Species listed	Synonymy included	Higher classification	Stratigraphic resolution	Geographic location	Hard/CD/Web	Updated	Reference
All taxa	Family	n/a	No	No	Yes	Stage	Yes	Hard/Web	No	Benton 1993
Marine animals	Genus	n/a	No	part	part	Stage	No	Hard/CD	?	Sepkoski 2002
Marine animals	Family	n/a	No	No	Yes	Stage	No	Hard	No	Sepkoski 1992
Fungal spores and mycelia	Species	Species	Yes	Yes	No	Stage	No	Hard	No	Kalgutkar and Jansonius 2000
Dinoflagellates	S (var)	n/a	Yes	Yes	No	Variable to Stage	No	Hard	Yes	Williams <i>et al.</i> 1998
Dinoflagellates	Species	Species	Yes	Yes	No	Variable to Stage	Yes	Hard	Yes	Cramer and Díez (1979)
Acnitarchs	Species	n/a	Yes	Yes	No	Variable to Stage	No	Hard	No	Fensome <i>et al.</i> 1990
Palynomorphs	Species	Species	Yes			Stage	Yes	Hard	Yes	Jansonius and Hills 1978
Foraminifera	Genus	Genus	Yes	Yes	Yes	Stage	Yes	Hard	No	Loeblich and Tappan 1988
Invertebrates	Species	Genus	Type	Yes	Yes	Stage	Yes	Hard	Yes	Moore 1955
Echinoids	Species	Genus	Yes	Yes	Yes	Stage	Yes	Hard/Web	Yes	< www.nhm.ac.uk/science/echinoids >
Echinoids	Species	No	Yes	No	Yes	Stage	Yes	Hard	No	Kier and Lawson 1978
Fishes	Species	Genus	Yes	part	Yes	Stage	Yes	Hard	No	Schultze 1978
'Reptiles'	Species	S	Yes	Yes	Yes	Stage	Yes	Hard	No	Kuhn 1969
Birds	Species	No	Yes	Yes	Yes	Epoch	Yes	Hard	No	Brodcorp 1963–1978
Mammals	Genus	No	No	Yes	Yes	Epoch	Yes	CD	No	McKenna and Bell 1997
Land plants	Species	Species	Yes	Yes	Yes	Variable to Stage	Yes	Hard	No	Boureau 1964–1975
Plants	Species	Species	Yes	No	Yes	Stage	Yes	Web	No	< http://fibs.ucl.ac.uk/fibs >

and ctenoids make up what we now know as the teleosts — the dominant group of fishes today. Woodward recognized 387 fossil species in 190 genera while Agassiz recognized 342 fossil species in 173 genera. The comparison is remarkable. And if we compare the actual names of the genera we find that out of Woodward's 190 generic names 75, or 40%, are shared with Agassiz names. And some of those that were not shared were only minor changes in name such as Woodward preferring to refer to the fossil form as Eo- or Pro- rather than Agassiz' preference to refer fossil species to Recent genera whenever he thought possible.

TABLE 2. Recognition of genera and species of fossil fishes according to Louis Agassiz and Arthur Smith Woodward. (A) For all fossil fishes. (B) For the teleost fishes. See text for discussion.

A	Genera		Species		Species per genus	
	Agassiz	Woodward	Agassiz	Woodward	Agassiz	Woodward
placoids	81	97	406	341	5	3.5
ganoids	94	104	475	439	5	4.2
cycloids	86	95	178	218	2.1	2.3
ctenoids	87	95	164	169	1.9	1.8
Totals	348	391	1223	1167	3.5	3
B	Genera		Species			
	Agassiz	Woodward	Agassiz	Woodward		
cycloids	86	95	178	218		
ctenoids	87	95	164	169		
Totals	173	190	342	387		

But the situation is far worse with species. There was, in fact, very little overlap in the species names. Woodward had sunk most of Agassiz' into synonymy and erected many new ones. This may give us a message, at least for paleontology. Species names are far more labile, far more difficult to apply in systematic revisions, and, in effect, far more difficult to document. This is because species boundaries are far more ambiguous than genera, etc.

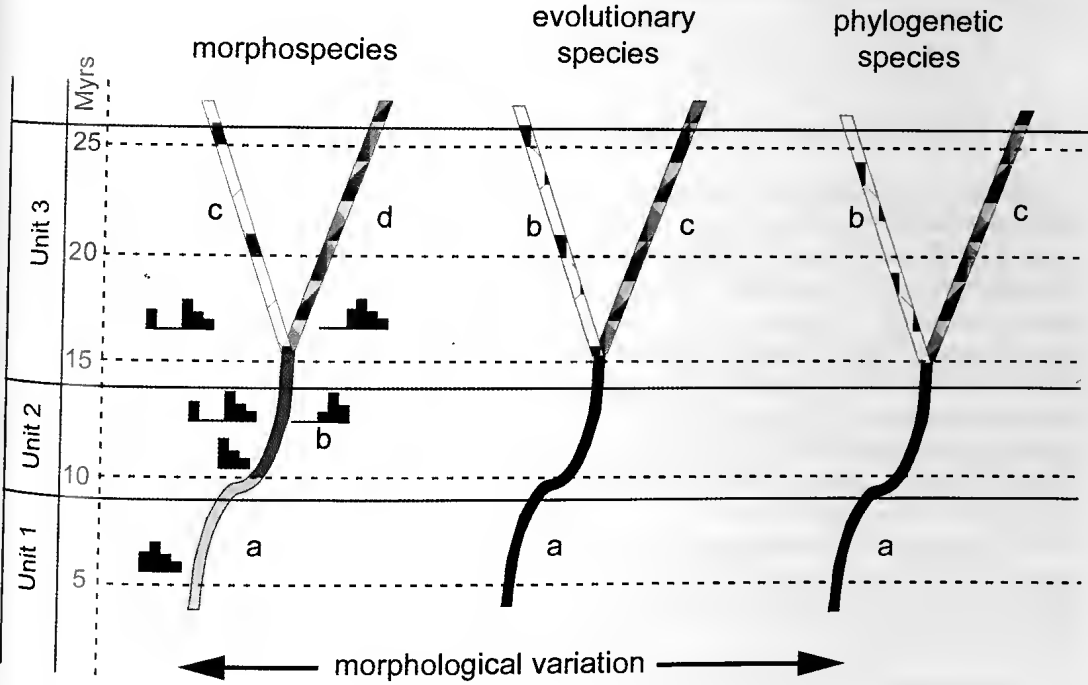
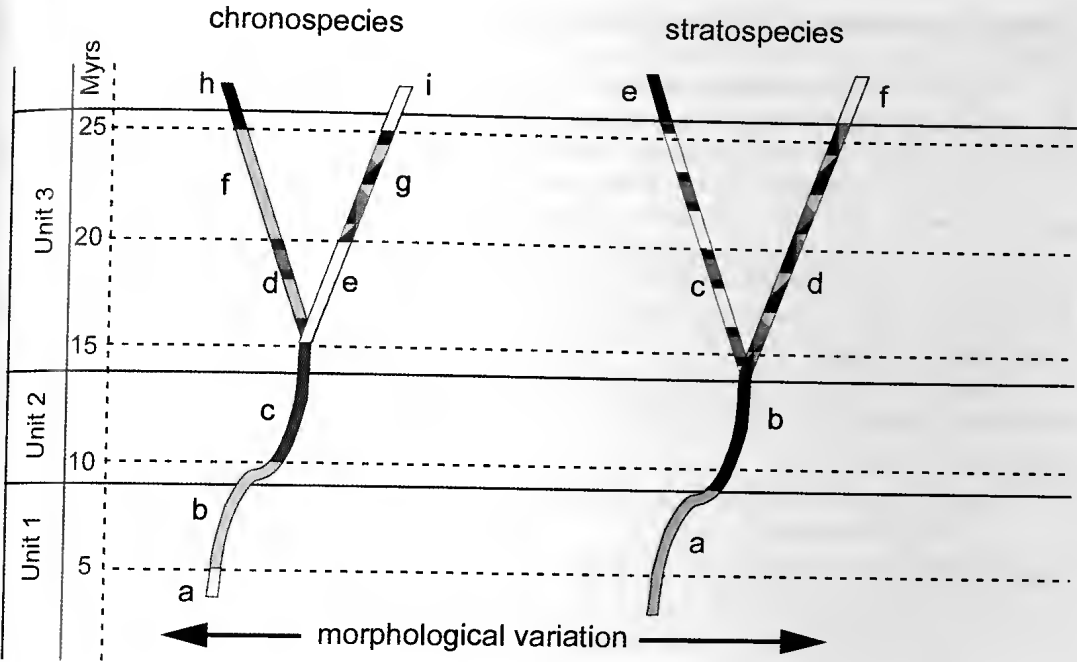
Paleontological species come in many guises, mostly due to the fragmentary nature of fossils, which are always incomplete in some way or other. Even if they are complete we generally do not have the geographic sampling or ontogenetic continuity to truly say whether we have one or more species. There are, of course, echoes of this in the Recent world but the resonance is far greater in paleontology.

Different species names have often been given to different parts of animals found isolated. For plants this is particularly true where the fructifications, stems, roots, leaves and spores are each given separate names as form taxa.

For paleontologists there is an additional dimension when we consider the time aspect of fossils. The problem of recognizing species is exacerbated because there are different ways to divide a stratigraphic continuum, based on different concepts of species and leading to different species recognition and the names applied (see Forey, *et al.* 2004). Sometimes this is done by simply dividing the continuum in segments of equal time — the chronospecies. Others give different species names where the continuum intersects with a stratigraphic boundary or sometimes with a break in the succession — the stratigraphic species. Others divide the continuum into segments according to the degree of variation seen in the modern representatives, should there be any. Yet others divide the continuum according to deviations in morphological trends — the evolutionary species concept of George Gaylord Simpson, while others will give new species names only at inferred cladogenetic events — the phylogenetic species concept.

Clearly, with such a multitudinous variety of species concepts and recognition criteria, the units to which we give species names have to be regarded with suspicion and the calculations of species duration through time must also be regarded with great care. Many of these problems, such as form taxa, with different species representing parts of the same organism or stages of life histories will be difficult to overcome. Their solution depends upon fortuitous finds of fossils. However, it is reasonable to suggest that the concepts of chronospecies, stratigraphic species, evolutionary species, and phylogenetic species be discouraged, and that species be established and named on unique combinations of characters as advocated by Wheeler and Platnick (2000). This will allow closer comparison with Recent species that, despite the domination of the biological species concept, are most often recognized on combinations of morphological characters. By doing so, esti-

FIGURE 3 (right). Species problems in paleontology. There have been various ways in which lineages of fossils traced through the rocks have been partitioned into species. Both the different implied theoretical concepts and the different practical ways in which this is done lead to very different concepts of species. In this diagram five concepts are shown against a common background showing a lineage of fossils collected from successively earlier strata in which the morphology (horizontal axis) changes and at one point diverges into two distinctive morphotypes. Thick continuous lines are stratigraphic boundaries; dotted lines are subdivision into equal time bands. Top diagram: two concepts which depend exclusively on the time aspect. The chronospecies is recognized as units delimited by arbitrary units of time (in this case every five million years). The stratospecies is delimited at stratigraphic boundaries. Lower diagram: three concepts centered on the intrinsic morphological variation. The morphospecies is recognized when overall morphology or some morphological variable has changed through time sufficiently to consider a new species (the histograms represent some measure of variation of populations). The evolutionary species recognizes species boundaries where some evolutionary trend changes beyond that expected from stochastic variation. The phylogenetic species is recognized only when a cladogenetic event takes place.



mates of species longevity can be compared in a more realistic way with likely fates of modern species.

At the end of the day disagreements over recognizing species, at least in the fossil record, may be counterproductive to effective production of taxonomic information, web-based or otherwise. Full species listings for many groups are just not feasible propositions. Listings at the generic level are possible and achievable. On the whole, genera are recognized on clear-cut characters such as presence/absence characters that can be evaluated more easily than those used at the species level — which are often proportions and counts of parts, patterns of ornament, colour patterns etc. And for this reason alone I would advocate maintenance of the Linnean binomial. Descriptions at the generic level would be given, still tied to the type species and the type specimen — both of which I recommend we keep.

When my colleagues and I sat down to discuss web-based taxonomy (Forey et al. 2004) we all agreed that paleontology would benefit for exactly the same reasons that are cited by neontological taxonomists, namely:

1. Web-based taxonomic databases can significantly reduce the time lag between the acquisition and dissemination of knowledge.
2. The ability to constantly update taxonomic data is an obvious advantage of the web.
3. Pertinent primary literature for fossil genera and species is scattered through a huge number of books and journals, many of them restricted to specialist libraries. If basic taxonomic information can be placed on the web, it will help standardise the use of names by allowing easier access to critical data by a larger number of people. Technically, it would be possible to include tracts of text and illustrations from the relevant original literature, but this demands cognisance of copyright laws.
4. Web-based lists make it potentially easier to collate information (i.e., numbers of genera/species from named horizons etc) with the possibility of calculating rates of origination and extinctions (e.g., this is now possible with the web-based Fossil Record II, Benton 1993).
5. The description of fossil taxa can often involve reference to many different partial specimens in order to capture the complete morphology. The unlimited space for illustration on the www is clearly an advantage. However, there remains no substitute for examining actual specimens.

There are some potential disadvantages of a web-based taxonomy, but none are unique to paleontology. The main problem to be solved is how web-based taxonomy is to gain validation. Taxonomic data can be posted on the www without passing through any review process and thereby run the risk of erecting poorly diagnosed taxa. It might be necessary to establish accredited host sites and/or panels of experts who could ensure quality control, however authoritarian this may seem. No such system currently exists and the erection of such panels would not be an easy exercise in a science where individuals have had free reign. Perhaps, like journals, the respect for some web sites may become self-regulating. The best taxonomy has always come from individuals with the experience and breadth of knowledge to provide an authoritative overview — Agassiz and Woodward once again. It is probable that data-rich and scientifically useful sites will soon become self-evident to the wider community.

An important consideration of www-based reference taxonomy is the feasibility of its goals. Many web sites have started, only to fizzle out. For the www to be any advantage over our current vehicles for disseminating taxonomic information it must capitalize on its strengths, accessibility and instantaneousness.

I have pointed out above that taxonomic problems associated with defining species are far more complex than those associated with genera and monophyletic clades. Species-level taxonomy usually requires data on large numbers of individuals and is often based on very subtle charac-

ter assessments. Consequently, species boundaries are rarely unambiguous and obvious. By contrast, generic and higher taxonomic levels are usually established on the basis of more major character traits that are easier to define and illustrate. Whereas a web-based taxonomy at genus level and above may be relatively easily achieved, the goal of placing all species on the web seems over-ambitious given present resources devoted to taxonomy.

SUMMARY

I would maintain that despite shedding the theoretical basis of Linnaeus we have and indeed need to retain the binomial, type species and type specimen. I would advocate recognition of species based on unique combinations of characters and reject the chronospecies, stratospecies, evolutionary species (of Simpson) and phylogenetic species as useful entities by which to name the world. I would further recommend that it be mandatory for an author to designate the phylogenetic status of genera and more inclusive taxa, irrespective of whether rank is applied or not.

With respect to any future taxonomic compilations that may be put on the Web (www), we should concentrate our efforts on revision and documentation on genera, rather than species.

The biggest challenge over the next few years will be to devise methods for validating web-based taxonomy. Certainly the international codes of nomenclature will have to change to give guidance on naming genera and species on the Web. There needs to be a clear distinction between authoritarianism, which will simply fragment our science of taxonomy, and authoritiveness which will secure its future.

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A Unified Concept of Species and Its Consequences for the Future of Taxonomy

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Contemporary species concepts are diverse. Nonetheless, all share the fundamental idea that species are segments of lineages at the population level of biological organization. They differ in the secondary properties (e.g., intrinsic reproductive isolation, monophyly, diagnosability) that are treated as necessary for considering lineages to be species. A unified species concept can be achieved by interpreting the common fundamental idea of being a separately evolving lineage segment as the only necessary property of species and viewing the various secondary properties either as lines of evidence relevant to assessing lineage separation or as properties that define different subcategories of the species category (e.g., reproductively isolated species, monophyletic species, diagnosable species). This unified species concept has a number of consequences for taxonomy, including the need to acknowledge that undifferentiated and undiagnosable lineages are species, that species can fuse, that species can be nested within other species, that the species category is not a taxonomic rank, and that new taxonomic practices and conventions are needed to accommodate these conclusions. Although acceptance of a unified species concept has some radical consequences for taxonomy, it also reflects a change in the general conceptualization of the species category that has been underway for more than a half-century — a shift from viewing the species category as one member of the hierarchy of taxonomic ranks to viewing it as a natural kind whose members are the units at one of the levels of biological organization. This change is related to a more general shift in the primary concern of the discipline of systematics (including taxonomy), from the utilitarian activity of classifying organisms to the scientific activity of testing hypotheses about lineage boundaries and phylogenetic relationships. The unified species concept is a natural outcome of this conceptual shift and represents the more complete acceptance of the idea that species are one of the fundamental units of biology. As such, the unified species concept is central to the future of taxonomy.

It is widely held that species are one of the fundamental units of biology (e.g., Mayr 1982; Ereshefsky 1992; Claridge et al. 1997). Any time biologists compare different organisms, they consider it critical whether those organisms come from the same or from different species. In fact, they often consider their studies to be comparative only if those studies involve multiple species. Moreover, species are used as units of comparison in virtually all fields of biology — from anatomy, to behavior, development, ecology, evolution, genetics, molecular biology, paleontology, physiology, and systematics (including taxonomy). Species are considered so important that biologists have developed a formal system of rules for naming them, which they use in an attempt to give each and every species its own unique name (e.g., ICZN 1999; IBC 2000).

According to some authors, the concept of species is not only one of the central concepts of biology but also one of that discipline's oldest and most vexing problems (e.g., Dobzhansky 1976). The problem is that biologists have been unable to reach a general agreement about the nature of species and thus about the definition of the species category. Many papers have been written about this topic, and many definitions (i.e., descriptions of species concepts) have been proposed, but despite all the attention that species concepts have received, no single definition (or its corresponding concept) has proved optimal for all of the different uses to which biologists put the term. As a consequence, although one definition or concept has often come to predominate for a certain period of time, or among a certain subgroup of biologists, no single definition or concept has become universal within biology as a whole. This lack of agreement about the concept of species has come to be known as "the species problem" (e.g., Mayr 1957; Dobzhansky 1976).

In this paper, I will review a proposed solution to the species problem that unifies diverse contemporary views on the nature of species (de Queiroz 1998, 1999). The solution is based on identifying a common element in the diverse contemporary views about the nature of species, which not only clarifies the nature of the species problem but also suggests a straightforward solution, the result of which is a unified concept of species. After describing this unified species concept, I will consider some of its consequences, arguing that several have been foreshadowed by recent developments in the study of species. Finally, I will discuss how the unified concept of species represents the more complete acceptance of a historical shift in the conceptualization of the species category that is already widely held among biologists.

Because of the theoretical importance of species and the unresolved nature of the species problem, a unified concept of species is critical to the future of taxonomy. I hope that my proposal will contribute to ending the long-standing debate about the nature of species (see also O'Hara 1993, 1994; Pigliucci 2003) so that biologists in general, and systematists in particular, can focus their attention on methods for determining the boundaries of species (e.g., Sites and Marshall 2003), the processes responsible for the diversification of species (e.g., *TRENDS in Ecology and Evolution*, July 2001), and the enormous task of inventorying the species of the world (as discussed in the papers from the *Biodiversity* symposium included in this volume).

THE DIVERSITY OF CONTEMPORARY SPECIES CONCEPTS

Most systematic and evolutionary biologists are familiar with the existence of alternative species concepts. Many readers may be surprised, however, by the number of different concepts that have been proposed. Mayden (1997, 1999), for example, listed 24 named species concepts. As a point of departure, I will adopt a taxonomy that recognizes 13 major categories of species concepts and their corresponding definitions (some of which are subsets of others), based on properties that distinguish the different concepts from one another (Table 1). Space prohibits me from describing these alternative species concepts in detail, so I refer readers to Mayden (1997) and de Queiroz (1998) for reviews. I hope that readers are familiar with at least a couple of the different concepts, though such familiarity is not necessary to follow my arguments. What is important is to know two general things.

First, the different species concepts and their corresponding definitions are based, in part, on different biological properties. For example, the biological species concept is based (in part) on reproductive isolation, the ecological species concept is based on the occupation of a distinct niche or adaptive zone, one version of the phylogenetic species concept is based on diagnosability, and another version is based on monophyly. The second important thing to realize is that many of the different species concepts are incompatible with one another in that they lead to the recognition of different species taxa — that is, to different species boundaries and, thus, to different numbers of

TABLE 1. Alternative species concepts and the properties that distinguish them (after de Queiroz 1998). Indented concepts are subsets (not necessarily mutually exclusive) of the non-indented concept immediately preceding them.

<i>Species Concept (Traditional Name)</i>	<i>Distinctive Properties (Species Criteria)</i>	<i>Advocates Proposing Explicit Species Definitions</i>
Biological	Potential interbreeding/Intrinsic reproductive isolation	Wright (1940); Mayr (1942, 1963); Dobzhansky (1950)
Isolation	Isolating mechanisms	Mayr (1942, 1963); Dobzhansky (1970)
Recognition	Compatible mate recognition and fertilization systems	Paterson (1978, 1985)
Evolutionary	Unitary evolutionary role, tendencies, and fate	Simpson (1951, 1961); Wiley (1978, 1981)
Ecological	Distinct adaptive zone (niche)	Van Valen (1976)
Cohesion	Intrinsic cohesion mechanisms	Templeton (1989)
Phylogenetic	Association with Phylogenetic Systematics (Cladistics)	See below
Hennigian	Species bounded at both ends by cladogenetic (lineage splitting) ¹	Hennig (1966); Ridley (1989)
Monophyletic (Apomorphic)	Monophyly (as evidenced by apomorphies = derived character states)	Rosen (1979); Mishler (1985)
Diagnosable	Diagnosability (possession of fixed character state differences)	Cracraft (1983); Nixon and Wheeler (1990)
Genealogical ²	Exclusive coalescence of alleles for multiple loci	Baum and Shaw (1995)
Phenetic	Phenetic cluster (group of similar organisms separated by gaps from other such groups)	Michener (1970); Sneath and Sokal (1973)
Genotypic Cluster	Deficit of genotypic intermediates (heterozygotes) at multiple loci	Mallet (1995)

¹ Species can also be bounded at one end by extinction.

² The genealogical species concept could be considered an example of the monophyletic species concept (rather than a mutually exclusive concept) in that exclusive coalescence is equivalent to one interpretation of monophyly (see de Queiroz and Donoghue 1990). On the other hand, the monophyletic version of the phylogenetic species concept is usually concerned with monophyly as it relates to component populations or organisms rather than alleles.

recognized species. For example, it is commonly the case that adopting the diagnosable version of the phylogenetic species concept leads to the recognition of many more species taxa than would be recognized under the biological species concept (e.g., Cracraft 1983; Zink 1996). This situation creates a problem given that species are used as basic units of comparison in diverse types of studies. On the one hand, if a researcher were to use the species taxa recognized by several different authors specializing on different taxonomic groups, those species taxa likely would not be equivalent to one another. On the other hand, if a researcher were to use species taxa based on a single species concept, that person might obtain a very different result than if he or she were to use species taxa based on a different species concept.

The existence of alternative and incompatible species concepts reflects a basic disagreement about the nature of species (though, as I will argue below, there is also considerable agreement). This situation may not be particularly troubling to an individual researcher who is convinced that one of the concepts is superior to the others. The problem is that other researchers exhibit equal conviction in their commitments to different species concepts. In addition, the situation is getting worse rather than better, which is to say that the number of alternative species concepts is increasing, rather than decreasing. Of the 24 concepts listed by Mayden (1997), a full one-third were proposed in the preceding ten years. Moreover the biological species concept, which was once the dominant concept and is still perhaps the most widely adopted, seems to be less popular now than it was 30 years ago.

The existence of diverse species concepts makes a certain amount of sense, because the different concepts are based on properties that are of greatest interest to different subgroups of biologists. For example, biologists who study hybrid zones tend to emphasize reproductive barriers, systematists tend to emphasize diagnosability and monophyly, and ecologists tend to emphasize niche differences. Paleontologists and museum taxonomists tend to emphasize morphological differences, and population geneticists and molecular systematists tend to emphasize genetic ones. In addition, the biological properties that are most important in determining the limits of species likely differ among taxonomic groups (e.g., birds versus cyanobacteria), and this situation likely influences the properties emphasized by biologists who specialize on different groups. Nevertheless, for those researchers who are able to step back from their own personal investments and research interests, all of the concepts seem to have some merits in that they are all based on important biological properties (Table 1).

RECONCILIATION

The reconciliation of these diverse views has two basic components (de Queiroz 1998, 1999). The first is identifying a common fundamental element shared by all modern species concepts. The second is re-evaluating the differences among alternative species concepts in the context of this common element. Before I describe this solution to the species problem, I want to say that regardless of whether one accepts my proposal, a solution is unlikely to come from the general approach that people have been taking for the last 50 years. I refer to the approach of identifying a particular biological property — whether reproductive isolation, ecological distinctiveness, monophyly, diagnosability, or anything else — as the basis of a species concept, and then advocating that concept because of its supposed theoretical and/or operational superiority over rival concepts. That approach is unlikely to succeed, and it certainly has not been successful so far. Rather than solving the species problem, it has caused (and later aggravated) the problem. Rather than leading to agreement on a single species concept, it has led to a proliferation of alternative concepts and more disagreement than ever. For this reason, I have taken a completely different approach. Instead of proposing yet another species concept based on yet another biological property, I have proposed a way to unify the existing species concepts.

The Common Element

Previous attempts to solve the species problem have tended to obscure the solution by emphasizing the differences, rather than the similarities, among alternative species concepts. As it turns out, all contemporary species concepts share a common element, and more importantly, that shared element is fundamental to the way in which species are conceptualized. Virtually all contemporary species concepts equate species with populations or population lineages — or more accurately, with segments of population level lineages.

LINEAGES: Because the concept of a lineage is central to my proposal, I need to clarify some things about lineages. When I use the term lineage, I am not talking about a clade or a monophyletic group (see de Queiroz 1998, 1999), and thus, I am not advocating a version of the phylogenetic species concept. A lineage, in the sense that I am using the term (see also Simpson 1951; Hull 1980), is a line of direct ancestry and descent (Fig. 1). Such lineages commonly are not monophyletic in that their later members or parts share more recent common ancestors with recently diverged side branches (which are parts of different lineages) than they do with earlier members of the same lineage. Lineages are formed by biological entities at several different levels of organization. For example, every person can trace his or her ancestry back along an organism lineage that passes through a series of ancestral organisms — a parent, a grandparent, a great grandparent, and so forth. Similarly, each species can trace its ancestry back along a population level lineage that passes through a series of ancestral species.

I also want to point out that lineages, not only population level lineages but also those at other levels of biological organization, are the entities that actually evolve (Hull 1980). In fact, I have argued (de Queiroz 1999:82) that the common claim that populations, rather than organisms, are the entities that evolve (e.g., Futuyma 1986:7), which is reflected in the common definition of evolution as changes in gene frequencies in populations (see Mayr 1982:400), is attributable to the temporal extendedness, rather than the organizational level, of populations. Even if organisms themselves do not evolve, organism lineages do evolve, and this conclusion suggests that evolution can be defined generally as heritable changes in lineages. (This definition is conceptually similar to Darwin's descent with modification but incorporates the requirement that the modifications must be heritable. It includes gene frequency changes in populations as a special case.) Thus, the concept of a lineage is fundamental to the concept of evolution itself, and it also turns out to be common to all species concepts formulated in the context of an evolutionary worldview.

Because lineages at the species/population level are made up of several species, species themselves are segments of such lineages. The diagrams in Figure 2 illustrate this point in the context of three general models of speciation (Foote 1996). In these diagrams, the vertical lines represent species, and the horizontal ones represent speciation events. In the bifurcation model, where ancestral species become extinct at speciation events, species correspond more or less precisely with the lineage segments between those events. In the budding model, where ancestral species persist

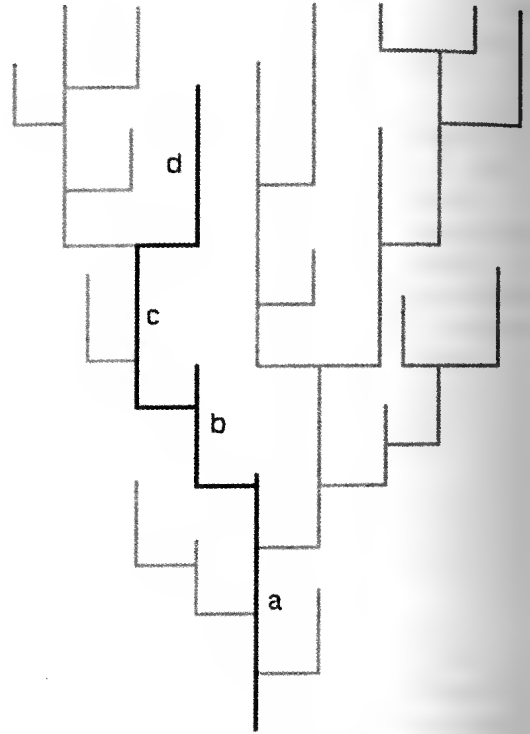


FIGURE 1. Representation of a species (population) level lineage and its component species within a larger branching tree (modified from de Queiroz 1999). The lineage of interest, represented by the darker lines, is made up of a series of ancestral and descendant species, labeled with the letters a through d. Note that the lineage is not monophyletic in that some of its later members (e.g., species 'd') share more recent common ancestors with recently diverged side branches (gray lines) than with earlier members of the lineage (e.g., species 'a').

through speciation events, the lineage segments that correspond with species originate, but don't necessarily terminate, in those events. Finally, in the phyletic transformation model, where speciation occurs within an unbranched lineage, species once again correspond more or less precisely with the lineage segments between speciation events, though what counts as a speciation event differs from the other two models. In the bifurcation and budding models, speciation corresponds with lineage splitting (cladogenesis), while in the phyletic transformation model, speciation corresponds with change within an unbranched lineage (anagenesis). With the exception of speciation via hybridization (which might be considered a variant of the budding or bifurcation models, depending on how it occurs),

these three general models cover the range of possibilities, and all contemporary species concepts are consistent with (and sometimes imply) one or more of them. Notice that in all three models, species correspond not with entire lineages but instead with lineage segments.

As I pointed out earlier, biological entities at various organizational levels form lineages — from genes, to organelles, cells, organisms, and species. The lineages at each level are made up of lower level lineages. Thus, each population level lineage is made up of several organism lineages. In the case of sexual or biparental reproduction, the process of reproduction itself unites organism lineages to form a higher (population) level lineage, because the organism lineages come together at each reproductive event to form an anastomosing nexus. In the case of asexual or uniparental reproduction, the organism level lineages are not bound together in this manner. Therefore, if unification of asexual organism lineages occurs, it must result from other processes than reproduction. Whether asexual organisms do in fact form such higher level lineages is controversial, but the answer is not important to my argument. What is important is that species definitions that are intended to apply to asexual organisms assume that they do.

With these clarifications in mind, let me reiterate that all contemporary species concepts are variations on the general theme that species are segments of population-level lineages. Here, I am using the term population in a very general sense that refers to a level of organization above that of the organism, and which applies — at least potentially — to both sexual and asexual beings. I have previously referred to this common theme as the general lineage concept of species to emphasize that the concept of the population level lineage is general in the sense of being common to all contemporary species concepts (de Queiroz 1998, 1999). It is important to understand that this gen-

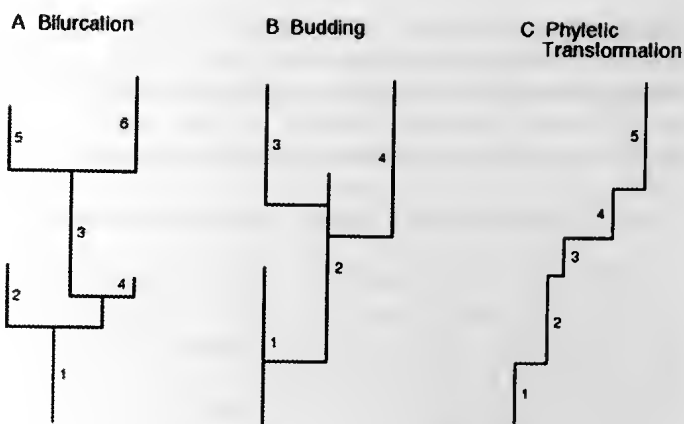


FIGURE 2. Three general models of speciation (modified from Foote 1996). A. Bifurcation model, in which speciation corresponds with lineage splitting and ancestral species terminate upon giving rise to two descendants. B. Budding model, in which speciation corresponds with lineage splitting and ancestral species persist after giving rise to one or more descendants. C. Phyletic transformation model, in which speciation corresponds with change in an unbranched lineage and ancestral species terminate after transforming into descendants. The budding and bifurcation models can be classified as cladogenetic models, in which speciation corresponds with lineage splitting; the phyletic transformation model can be classified as an anagenetic model, in which speciation corresponds with change in an unbranched lineage. Vertical lines represent species; horizontal lines represent speciation events. That which constitutes a speciation event is deliberately left undefined to accommodate diverse species concepts.

eral lineage concept is not an alternative to the various contemporary species concepts; instead, it is a more general concept that subsumes all of them. An early example of a species concept conforming to the general lineage concept can be found in Darwin's (1859) *Origin of Species*, where species are described and illustrated as "lines of descent." More importantly, the general lineage concept underlies virtually every species concept described during the last half century.

The Conformity of Diverse Species Definitions to the General Lineage Concept

I have previously presented evidence that diverse modern views on the nature of species all conform to the general concept of species as segments of population-level lineages (de Queiroz 1998, 1999). The following list summarizes this evidence for a diversity of papers proposing explicit species definitions (those used as the source of quoted species definitions in de Queiroz 1998). It is organized in terms of the nature of the evidence, which can be divided into five categories:

1) Papers that explicitly equate species with lineages in their proposed species definitions. Examples are the evolutionary definitions of Simpson (1951, 1961) and Wiley (1978, 1981) and the ecological definition of Van Valen (1976), all of which begin with some variant of the phrase "a species is a lineage."

2) Papers that explicitly equate species with lineages in their extended discussions, as opposed to their concise definitions. Examples are Mishler's (1985) and Nixon and Wheeler's (1990) papers describing different versions (monophyletic and diagnosable) of the phylogenetic species concept, Ridley's (1989, 1990) on the cladistic (Hennigian) species concept, Templeton's (1989, 1998) on the cohesion species concept, and Baum and Shaw's (1995) on the genealogical species concept.

3) Papers that represent species as lineages using diagrams. In these diagrams, species are represented either as single lines (e.g., Darwin 1859, figure 1) or trunks (e.g., Hennig 1966, figures 14, 15), and their component organisms (if they are also illustrated) are represented by dots, which may be connected by lines representing relationships of descent and thus illustrating organism-level lineages (e.g., Hennig 1966, figures 3, 4, 6). Examples of such diagrams can be found in numerous papers, including (among those presenting explicit species definitions) those by Simpson (1951, 1961), Hennig (1966), Wiley (1981), Ridley (1989), Nixon and Wheeler (1990), and Baum and Shaw (1995).

4) Papers that implicitly equate species with lineages by equating them with populations in their proposed species definitions. As Simpson (1951) pointed out, a lineage is a population extended through time, and conversely, a population is a segment, in some cases an instantaneous cross section, of a lineage (see Simpson 1951, figure 3). Thus, definitions that equate species with populations and those that equate species with lineages simply represent time-limited and time-extended versions of the same general species concept. Examples include Wright's (1940), Mayr's (1942, 1963, 1982), and Dobzhansky's (1950, 1970) definitions of the biological species concept, Rosen's (1979) apomorphic version of the phylogenetic species concept, and Paterson's (1985) recognition species concept.

5) Papers that implicitly equate species with lineages by equating them with populations in their extended discussions. Examples include Cracraft's paper on the diagnosable version of the phylogenetic species concept (1983), Michener's (1970) and Sneath and Sokal's (1973) writings on the phenetic species concept, and Mallet's (1995) paper proposing the genotypic cluster species definition.

Even those modern species definitions that seem to diverge most drastically from the rest are at least consistent with — if not actually based on — the general lineage concept of species. For example, phenetic species definitions describe species as phenetic clusters (e.g., Michener 1970; Sneath and Sokal 1973) rather than populations or lineages. These definitions do not, however,

contradict the equation of species with populations or lineages; instead, they simply emphasize the evidence and procedures that are used to recognize species in practice (e.g., Rogers and Appan 1969; Michener 1970; Sokal and Crovello 1970; Sneath and Sokal 1973; Doyen and Slobodchikoff 1974).

Similarly, species definitions that emphasize the property of monophyly (e.g., Rosen 1979; Donoghue 1985; Mishler 1985) seem to deny that species differ in any important respect from higher taxa or clades. The views underlying these definitions are also consistent with the equation of species with lineages. Advocates of the definitions in question stress the importance of monophyly; however, contrary to the way their views are sometimes portrayed, they do not require all species taxa to be monophyletic. They acknowledge that the members of a single species may not always be mutually most closely related in terms of their common ancestry relationships. The authors in question still refer to these lineages using species names; however, to call attention to their non-monophyletic status, they designate such species paraspecies (Ackery and Vane-Wright 1984), if the evidence suggests that they are paraphyletic, or metasppecies (Donoghue 1985; see also Graybeal 1995) if the evidence is equivocal.

DIFFERENCES AMONG ALTERNATIVE SPECIES CONCEPTS

Once we realize that all contemporary species concepts share the common view that species are segments of population-level lineages, the next problem is to explain how it is that so much disagreement about species concepts can exist in spite of this general agreement. The answer to this question becomes apparent when we consider the differences among alternative species concepts in the context of the common element. The answer is as follows: if we consider the common element — existence as a separate lineage — as the primary defining property of species (primary species criterion), then the diversity of species concepts can be accounted for by recognizing that each alternative species concept adopts a different property of lineages as a secondary defining property of species (secondary species criterion). In other words, under all species concepts, a species is a population lineage, but under the biological species concept, for example, the lineage also has to be reproductively isolated from other lineages. Under the ecological species concept, the lineage also has to occupy a different niche or adaptive zone. Under the phenetic species concept, it also has to form a phenetic cluster. Under the diagnosable version of the phylogenetic species concept, it also has to have a unique combination of character states. Other concepts adopt still other secondary properties.

SECONDARY PROPERTIES AND LINEAGE DIVERGENCE. The reason that these different secondary properties — these secondary species criteria — lead to incompatible species concepts is that they commonly arise at different times during the process of lineage divergence. Lineage divergence can be conceptualized in terms of a few general evolutionary processes — processes such as mutation, migration (or the reduction thereof), natural selection, and genetic drift. In contrast, the characters affected by those processes are highly diverse. They can be genetic or phenotypic; qualitative or quantitative; selectively advantageous, disadvantageous, or neutral. Moreover, they involve many different aspects of organismal biology — including genetics, development, morphology, physiology, and behavior.

With regard to the species problem, the important point is that changes in these characters lead to the acquisition of a number of different properties by diverging lineages. Thus, as two lineages diverge, they become phenetically (quantitatively) distinguishable. They become diagnosable in terms of fixed character states. Their genitalia, gametes, and developmental systems become incompatible. Their mate recognition systems diverge to the point where their component organ-

isms no longer recognize one another as potential mates. They evolve distinctive ecologies. And they pass through polyphyletic, paraphyletic, and monophyletic stages in terms of their component genes and organisms (Neigel and Avise 1986). These different properties are not all expected to evolve at the same time, nor are they necessarily expected to evolve in a regular order (de Queiroz 1998). The problem is that each different species concept adopts a different one of these properties as a defining (necessary) property of species. This situation is what causes the different species concepts — despite their general conceptual unity — to result in conflicting conclusions concerning which lineages deserve to be recognized as species. In short, although all contemporary species concepts equate species with segments of population lineages, different concepts treat different events in the process of lineage divergence as marking the beginnings of those segments.

Figure 3 is a highly simplified diagram representing the process of lineage divergence. The shades of gray represent the daughter lineages becoming more and more different from one another through time, and the numbered lines (1–8) represent the times at which they acquire different properties relative to each other — for example, when they become phenetically distinguishable, diagnosable, reciprocally monophyletic, reproductively incompatible, ecologically distinct, and so forth. This set of properties forms a broad gray zone within which alternative species concepts come into conflict. On either side of the gray zone, there will be unanimous agreement about the number of species. Before the acquisition of the first property, everyone will agree that there is one species, and after the acquisition of the last property, everyone will agree that there are two. But in between, there will be disagreement. Some people will draw the cutoff where loss or fixation of a character in one of the lineages makes them diagnosable. Others will draw the cutoff where the lineages develop an intrinsic reproductive barrier. Still others will draw the cutoff where both lineages form exclusive groups in terms of multiple gene trees. Moreover, disagreements will be exacerbated if further splitting and divergence (acquisition of earlier properties) occurs before some of the later properties are acquired. This is cause of the species problem. This is the reason that there are so many incompatible definitions of the species category despite widespread agreement about the general nature of species.

A UNIFIED SPECIES CONCEPT

On the other hand, the situation I have just described suggests a very simple solution to the

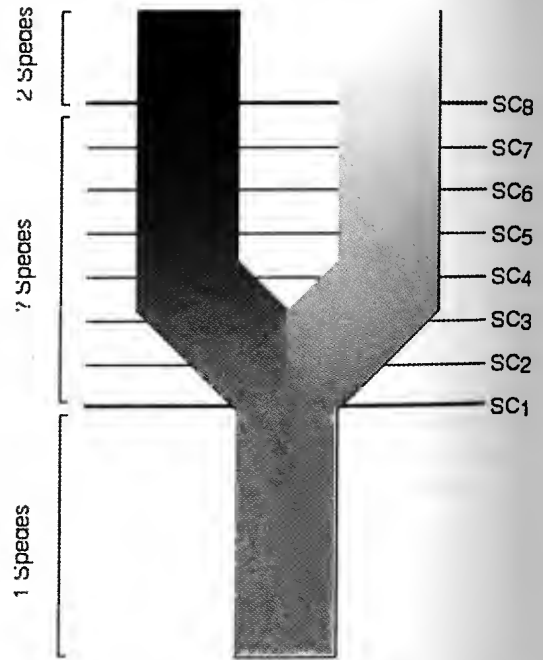


FIGURE 3. Lineage divergence and alternative species criteria (modified from de Queiroz 1998). The diagram represents the process of lineage divergence through a cladogenetic (lineage splitting) event. Progressive darkening and lightening of the daughter lineages represents their progressive divergence through time. The numbered horizontal lines (1–8) represent the times at which the daughter lineages acquire different properties relative to each other (e.g., when they become phenetically distinguishable, diagnosable, reciprocally monophyletic, reproductively incompatible, ecologically distinct, and so forth). The species problem results from disagreements about which of these properties are necessary (defining) properties of the species category (species criteria). The entire set of properties defines a zone in which there will be disagreement about the number of species among authors adopting different properties as their species criteria.

species problem. This solution involves a minor yet fundamental shift in the way we conceptualize species. It retains the element that is common to all contemporary species concepts, and it eliminates the conflicts between rival concepts without denying the importance of the properties that underlie their obvious differences. In short, it represents a unified species concept.

The solution has two components. First, we retain the common element — the general concept of species as separately evolving segments of population level lineages. In other words, we retain the primary species criterion. Second, we interpret this property as the only necessary property of species. In other words, we reinterpret all the other properties that have previously been treated as necessary properties of species — the properties that created the incompatibilities among alternative species concepts — as no longer being defining properties of the species category. They can be thought of instead as contingent properties: properties that species may or may not acquire during the course of their existence. In the context of this proposal, there are no secondary species criteria. Lineages do not have to be phenetically distinguishable, or diagnosable, or monophyletic, or reproductively isolated, or ecologically divergent, or anything else, to be species. They only have to be evolving separately from other lineages.

This unified species concept is related, but not identical, to the general lineage species concept. As noted above, the general lineage concept is the element that is common to all contemporary species concepts, which represent variations on this general theme. In addition, the general lineage concept is agnostic with regard to the differences among its variants, the alternative species concepts — that is, with regard to interpreting one or another secondary property of lineages as a necessary property of species. This agnosticism is necessary for the concept to be general — for it to subsume, rather than being an alternative to, the other contemporary species concepts. The unified species concept is based on the common element represented by the general lineage concept; however, in contrast with the general lineage concept and its variants, the unified concept treats the common element as the only necessary property of species. In other words, the unified species concept is not agnostic with respect to interpreting one or another secondary property of lineages as a necessary property of species; it rejects those interpretations. Nonetheless, the unified concept truly represents a unification in that it does not reject the diverse secondary properties themselves, recognizing that all of those properties continue to play important roles in the study of species.

Roles of Secondary Properties

I stated above that this proposed solution to the species problem eliminates the conflicts among rival species concepts without denying the importance of the properties that underlie their differences. Under a unified concept of species, the secondary properties — the former secondary species criteria — remain important in two ways. First, they continue to serve as important lines of evidence relevant to assessing the separation of lineages. These properties — properties such as phenetic distinguishability, reciprocal monophyly, pre- and post-zygotic reproductive barriers, ecological differences, and so forth — are, after all, some of the best available lines of evidence regarding lineage separation. However, in contrast with the focus on one or a few of these properties under one or another of the alternative species concepts, under the unified species concept, all of the properties are important. That is, the more lines of evidence that can be brought to bear on the question of lineage separation, the better.

Second, the secondary properties can be used to define subcategories of the species category — that is, to recognize different classes of species based on the properties that they possess. To use an organism level analogy, biologists commonly recognize different subcategories of the general category organism based on properties possessed by organisms. For example, they recognize sex-

ually mature organisms, fully grown organisms, socially dominant organisms, and so forth. Similarly, under a unified species concept, biologists would recognize different subcategories of the general category species based on properties possessed by species. For example, they might recognize reproductively isolated species, ecologically distinct species, monophyletic species, and so forth. (Incidentally, names based on the relevant properties, as in the preceding examples, describe these categories more clearly than do overly general terms such as biological species, ecological species, phylogenetic species, etc.) Thus, a unified species concept would not deny the importance of any of the properties that have been considered important by previous authors. It just would not treat those properties as necessary properties of species.

CONSEQUENCES OF A UNIFIED SPECIES CONCEPT

The solution to the species problem just outlined is very simple — so simple that one wonders if the reason it has been elusive has to do with an assumption that people have not thought to question. I will suggest that that assumption is related to the historical treatment of the species category as part of the hierarchy of taxonomic ranks, which has hindered biologists from fully accepting an important shift in the way they conceptualize the species category. I will return to this idea in the next section of this paper (*A Shift in the Conceptualization of Species*). In this section, I would like to address some consequences of a unified species concept.

I anticipate that some people are going to have difficulty accepting some of the consequences that I will describe, at least initially. The reason is that certain consequences of a unified species concept go against long-standing traditions — traditions that are related to the taxonomic assumption that I just mentioned. I would argue, however, that it is counterproductive to reject theoretical proposals simply because they conflict with taxonomic conventions. Given that the purpose of taxonomies is to convey (theoretically significant) information, it is more important for taxonomic conventions to be consistent with systematic theory rather than for systematic theory to be consistent with taxonomic conventions. Therefore, I ask readers to bear with me while I describe some consequences of a unified species concept. After I have finished describing those consequences, I will try to explain why biologists should accept them. Nevertheless, I will also describe how several of the consequences in question have been anticipated by recent trends in the way that biologists treat species.

All Lineages are Species

One consequence of adopting a unified species concept is that all separately evolving population level lineages are species. This conclusion follows directly from adopting the unified concept, which treats only existence as a separately evolving lineage, and not any of the contingent properties of lineages, as a necessary property of species. Thus, not only reproductively isolated lineages are species, nor only ecologically differentiated ones, nor only diagnosable ones, nor only phenetically distinguishable ones. Even undifferentiated and undiagnosable lineages are species. As long as a lineage exists, which is to say as long as it is (or was, in the case of an extinct lineage) evolving separately from other lineages, it is a species. And lineages can be separated by many different factors, including extrinsic (e.g., geographic) barriers. A corollary of this consequence is that there are many more species on Earth than biologists have been prepared to accept under traditional views. In addition to those species for which no organisms have yet been discovered, many of the species taxa that have been recognized under traditional species concepts are likely made up of multiple species.

This consequence of the unified species concept has been foreshadowed by a couple of recent

trends. One of these trends is related to the development of several of the alternative species concepts, according to which allopatric, diagnosable taxa formerly ranked as subspecies are regarded as species (e.g., Cracraft 1983; Frost and Hillis 1990). Given that the taxa in question are allopatric and diagnosable relative to other populations formerly considered conspecific with them, they presumably represent separately evolving lineages. If so, then their recognition as species is in agreement with the unified concept. This proposition should not, however, be misinterpreted as justification for treating all diagnosable units as species. For example, many recent studies based on mitochondrial DNA recognize groups of individuals or populations that are geographically contiguous and monophyletic (as well as diagnosable and phenetically distinguishable) in terms of their mtDNA haplotypes as species (reviewed by Avise 2000). Although several such groups within a previously recognized species may indeed correspond with separately evolving lineages, because mtDNA is maternally inherited, it is important to examine paternally or autosomally inherited genes to rule out the alternative hypothesis that the phylogeographic pattern results from female philopatry within a single lineage (Avise 2000).

Another recent trend foreshadowing the unified species concept is the recognition of "evolutionarily significant units" or "ESUs" within traditional species. Originally proposed in the context of conservation biology (Ryder 1986), an ESU is a population or set of populations that is morphologically and genetically, or evolutionarily, distinct from other populations. Several of the criteria proposed for ESU recognition, such as reciprocal monophyly for mtDNA alleles and significant divergence of allele frequencies at nuclear loci (e.g., Moritz 1994), correspond with secondary species criteria associated with some of the alternative species concepts (e.g., Baum and Shaw 1995; Highton 2000). Indeed, Vogler and DeSalle (1994) have explicitly proposed using the species criteria associated with one of the versions of the phylogenetic species concept (diagnosability criterion) for identifying ESUs. Given that these same criteria are lines of evidence used to infer the separation of lineages, many ESUs would likely be considered species under the unified species concept. This situation should be beneficial to conservation, given that many of the relevant regulations (such as the U.S. Endangered Species Act) emphasize species.

Species Fusion

Another consequence of a unified species concept is that species can fuse. Traditionally, it has been common to think of species as permanently or irreversibly separated lineages (e.g., Mayr 1982:296; Bush 1995). However, if all separately evolving lineages are species, then the separation of many species from other species may be temporary or reversible. This situation seems obvious for species that are separated only by extrinsic (i.e., geographic) barriers — at least ephemeral ones. However, it would also seem to hold for at least some cases in which separation is intrinsic (see below). As a consequence, collections of organisms or populations that form two species at a given time may fuse to form a single species at a later time.

This consequence is not unique to the unified species concept. It also holds under several of the alternative species concepts — in particular, those based on secondary criteria thought not to be indicative of permanent separation, such as distinguishability, diagnosability, and monophyly. Differences related to these properties commonly evolve between populations (lineages) separated by extrinsic barriers, leading to their recognition as separate species under the alternative species concepts in question. However, if those differences do not involve traits influencing reproductive compatibility (crossability of Mayr 1942), and if the extrinsic barriers subsequently disappear, then there is nothing to prevent the lineages from fusing.

Species fusion can also occur under secondary species criteria that are commonly thought to

be indicative of permanent separation — namely, intrinsic reproductive isolation (e.g., Mayr 1982). In the case of certain kinds of premating barriers, potential breakdown or reversal seems uncontroversial. For example, premating barriers based on ecological differences can break down if habitats change, which would seem likely to be a relatively common occurrence in the face of current large-scale, human-induced habitat changes. Moreover, in the case of postmating reproductive incompatibilities, it is at least theoretically possible for natural selection to eliminate the elements responsible for such an incompatibility, or for factors that reduce the deleterious effects of previously incompatible elements to evolve (e.g., Ritchie and Hewitt 1995). The realization that lineages exhibiting intrinsic reproductive isolation can fuse has been acknowledged by at least some advocates of a species criterion based on this property. Thus, Turner (2002), an advocate of the biological species concept (potential interbreeding criterion), explicitly acknowledged the possibility of species fusion, which he termed despeciation.

Species within Species

Another consequence of a unified species concept is that species can be nested within other species. Taxonomic tradition treats the species category as one rank or level in the hierarchy of taxonomic categories. In this context, taxa assigned to the same category (rank) are considered mutually exclusive (i.e., to have no members in common). As a consequence, taxa composed of more than one species must be assigned to higher ranks (such as subgenus or genus), and taxa within a species must be assigned to lower ranks (such as subspecies or variety). In other words, a species cannot be nested within another species.

This convention, however, is inadequate for dealing with many real biological situations involving species. In particular, it has problems with situations involving incomplete or partial lineage separation, as exemplified by cases of introgressive hybridization. These situations cause endless taxonomic problems under the traditional assumption that all taxa ranked as species are mutually exclusive and therefore cannot contain, or be contained within, other species. In such cases, taxonomies commonly vacillate between treating the partially separated lineages as the same species and treating them as different species. Some classic examples are found among North American birds, such as Bullock's (*Icterus bullockii*) and Baltimore Orioles (*Icterus galbula*) — Northern Orioles (*Icterus galbula*) when considered a single species — and Red-shafted (*Colaptes cafer*) and Yellow-shafted Flickers (*Colaptes auratus*) — Common Flickers (*Colaptes auratus*) when considered a single species (AOU 1998).

This problem can be remedied by allowing species taxa to be nested, a taxonomic innovation that is implied by the unified species concept. Contrary to traditional practice, the question of whether particular organisms belong to the same species cannot always be answered with a simple "yes" or "no." Sometimes lineages are only partially separated, which implies that their component organisms are simultaneously parts of both the same and different species. In other words, some species are nested within larger species. Moreover, such incompletely separated species do not have to be sister species to be parts of a single more inclusive species (see Omland, et al. 1999, for an example involving orioles).

The Species Category is Not a Rank

Another consequence of the unified species concept, which is related to several of the previous ones, is that the species category is not a taxonomic rank. Traditionally (i.e., under any of the alternative species concepts), only those separately evolving lineages that have evolved a particular secondary property (e.g., reproductive isolation, a distinct ecological niche, a unique combina-

tion of character states) are considered to merit taxonomic recognition as species. Other separately evolving lineages either are not granted formal taxonomic recognition at all, or they are assigned to a taxonomic category of lower rank, such as subspecies. This practice effectively treats both the species and subspecies categories as taxonomic ranks, which is in keeping with the taxonomic tradition in which the species category is a rank in the hierarchy of taxonomic categories (the rank below subgenus and above subspecies). It also has the undesirable consequence of ignoring or downplaying the significance of many separately evolving lineages.

Under a unified species concept, the species category is not a rank in the hierarchy of taxonomic categories but a class or kind made up of the entities or units at one of the fundamental levels of biological organization. Species are the entities that form lineages at the population level of biological organization just as organisms are the entities that form lineages at the organism level of biological organization (de Queiroz 1999). And just as all such entities at the organism level of organization are organisms (i.e., not only those that are postnatal, sexually mature, fully grown, etc.), similarly, all such entities at the population level of organization are species (i.e., not only those that are diagnosable, reproductively isolated, ecologically distinct, etc.). Because all separately evolving population level lineages are species, any taxa traditionally assigned to lower taxonomic ranks, such as subspecies and varieties, either are species, or they represent entirely different phenomena, such as morphs or artificial divisions in continuous patterns of geographic variation.

This consequence of the unified species concept has been foreshadowed by recent proposals, justified in the context of the evolutionary species concept (e.g., Simpson 1951, 1961; Wiley 1978, 1981), either to recognize former subspecies taxa as species (commonly subject to a secondary criterion of diagnosability) or to treat them as artificially defined parts of species (commonly as classes of organisms sharing one or more necessary and sufficient character states). For example, Grismer (2002), dealing with species of amphibians and reptiles inhabiting Baja California, recognized no subspecies whatsoever; instead, he treated all previously recognized subspecies either as species or as artificial "pattern classes" (see also Cracraft 1983; Frost 1995). Another manifestation of treating the species category as something other than a taxonomic rank is the view, to which I will return shortly, that the species category is fundamentally different from the other traditional taxonomic categories (e.g., Simpson 1961; Mayr 1969; see also de Queiroz 1997).

Current Taxonomic Conventions are Inadequate

All of the above conclusions suggest that traditional taxonomic practices are inadequate to accommodate a unified concept of species. Under such a concept, taxonomists will need to recognize many more species than are recognized in traditional taxonomies. They will need to recognize as species lineages that are separated now but may not be separated in the future. They will need to allow some species to be nested within other species (even if the former are not sister species). And they will need to stop treating the species category as a taxonomic rank. In short, taxonomists need new taxonomic conventions for representing the relationships among species, and they will also need new nomenclatural rules for governing the names of species.

Equally importantly, biologists need to be able to distinguish clearly and consistently between species that possess different properties — including both those that have previously been adopted as secondary species criteria (such as quantitative and qualitative differences, exclusivity, monophyly, ecology, and various kinds of reproductive barriers, from ecological and behavioral differences to incompatible genitalia and developmental systems) and those that have not (such as population size, type of population structure, amount or nature of genetic and phenotypic variation, and

others). Biologists need to come to terms with the fact that no single property of species is sufficient to address all of the diverse questions that species are used to answer. This means that biologists need to be able to identify — for any given study — those species possessing the property or properties that are relevant to answering the particular questions addressed in that study. Just as certain questions about organisms (e.g., those related to mating behavior) can only be answered using particular kinds of organisms (e.g., sexually mature ones), similarly, certain questions about species (e.g., those related to the phenomenon of reinforcement) can only be answered using particular kinds of species (e.g., those exhibiting postmating reproductive barriers). A species taxonomy — or even a traditional species database that includes information on geographic distribution and organismal traits — simply is inadequate for identifying the relevant species to use in a particular study. What is required is a species database that includes information on the diverse properties of species.

A SHIFT IN THE CONCEPTUALIZATION OF SPECIES

Some people are likely to have difficulty accepting at least some of the consequences of a unified species concept. Rather than trying to anticipate specific objections and presenting counterarguments, I will instead present a general perspective explaining how the unified species concept that I have described in this paper represents the more complete acceptance of an idea that is already widely accepted. The idea in question is a manifestation of a shift in the way that biologists conceptualize the species category that was well underway at least a half-century ago and has continued to gain ground, as indicated by the trends described in the previous section. Thus, even though some of the consequences of the unified species concept are at odds with taxonomic traditions, the concept itself is not particularly radical. It simply represents the next stage in an ongoing historical process. In this section, I will describe this shift in the conceptualization of the species category and how it relates to my proposed solution to the species problem.

Traditionally, the species category was one of the ranks in the hierarchy of taxonomic categories — the familiar kingdom, phylum/division, class, order, family, genus, and species — developed by Linnaeus (e.g., 1753, 1758) and other early naturalists. These categories were ranks that conveyed the relative inclusiveness of taxonomic groups (taxa): species were included within genera, genera within families, families within orders, and so forth. The taxa themselves, regardless of their rank, were all considered to be more or less the same kind of entities — groups of organisms sharing particular characters — some were just more or less inclusive than others. In other words, taxa assigned to the species category were not considered to differ fundamentally from those assigned to higher taxonomic categories; they were just smaller groups separated by smaller degrees of difference.

Darwin (1859) held the view of the species category that I have just described, though he provided an explanation both for the existence of the groups and for the differences among them. For Darwin, the species category was just another categorical rank — one that applied to groups of organisms differing more than varieties but less than genera. The following quotations from the *Origin of Species* illustrate Darwin's (1859) views on the species category and its relationships to the other taxonomic categories.

I look at the term species, as one arbitrarily given for the sake of convenience to a set of individuals closely resembling each other, . . . it does not essentially differ from the term variety, which is given to less distinct and more fluctuating forms (p. 52).

the natural system . . . is genealogical in its attempted arrangement, with the grades of acquired difference marked by the terms varieties, species, genera, families, orders, and classes (p. 456).

Some time after Darwin, a fundamental change occurred in how biologists viewed the species category. This change came to the forefront during the period of the Modern or Evolutionary Synthesis (e.g., Huxley 1942; Mayr and Provine 1980) in the middle of the 20th Century and formed the basis of what was then called the *New Systematics* (e.g., Huxley 1940). During this time, a new general concept of species emerged that resulted in a decoupling of the species category from the rest of the taxonomic hierarchy (de Queiroz 1997). Under this new view, species were conceptualized as inclusive populations (e.g., Wright 1940; Mayr 1942; Dobzhansky 1950), or as ancestor-descendant lineages of such populations (e.g., Simpson 1951, 1961). As a consequence, the species category came to be viewed as differing fundamentally from the higher taxonomic categories. The species category was no longer viewed simply as a taxonomic rank applied to entities of the same basic kind as genera and families; instead, the species category came to designate a particular kind of biological entity — the inclusive population or population lineage. In contrast, the higher taxonomic categories continued to be treated as ranks, which were now applied to more and less inclusive groups of species. The following quotations, from two of the great systematic biologists of the Synthesis Era, give evidence of this new view of species:

there are units in nature that have a special evolutionary status not fully shared with taxa either above or below them in the hierarchy . . . Many of them . . . recognized before Darwin had been called species, and it was inevitable that the term should be transferred to the evolutionary units (Simpson 1961).

The unique position of species in the hierarchy of taxonomic categories has been pointed out by many authors . . . It is the only taxonomic category for which the boundaries between taxa at that level are defined objectively (Mayr 1969).

This new view of species is perhaps epitomized in the statement by Mayr (1982:297) that “the species is as important a unit of biology as is the cell at a lower level of integration.”

The unified species concept described in this paper represents the more complete acceptance of the general conceptual shift just described — the shift from viewing the species category as a rank in the hierarchy of taxonomic categories to viewing the species category as a natural kind representing the units at one of the fundamental levels of biological organization. Conversely, this newer view of species reinforces the solution to the species problem represented by the unified species concept. My point is that if biologists are going to accept Mayr's proposition about species — if they are going to claim that the species is a fundamental category of biological organization, comparable to the categories cell and organism — then, to be consistent, they must adopt the unified concept of species. More specifically, they must discontinue the practice of treating certain secondary properties of lineages as necessary properties of species. Requiring population lineages to be diagnosable, or monophyletic, or reproductively isolated before those lineages are considered species is, to use an organism level analogy, like requiring living beings to be born, or sexually mature, or fully grown before they are considered organisms. Such a view not only prevents biologists from achieving a generally accepted definition of the species category, thus perpetuating the species problem, it also denies the species category the status of a fundamental category of biological organization and thus also of a truly central concept in biology.

CONCLUSION

The unified concept of species and the shift in the conceptualization of the species category that it represents bear on the history and the future of taxonomy. In one sense, taxonomy is among the oldest scientific disciplines. That is, taxonomy was among the earliest branches of human

knowledge to adopt explicit methods — to be approached systematically. In another sense, however, taxonomy has only recently become a science. Although the discipline of taxonomy has existed for a very long time, it has only recently experienced a shift from being primarily concerned with the utilitarian exercise of classifying to being primarily concerned with the scientific endeavor of testing hypotheses. Historically, taxonomists have been concerned with classifying organisms into groups based on shared traits, and then further classifying those groups into the categories of the taxonomic hierarchy, from kingdom to species. In contrast, modern systematic biologists, despite the fact that they still use data taking the same basic form of similarities and differences among organisms, are increasingly devoting their efforts to testing hypotheses about lineage boundaries and phylogenetic relationships. An important manifestation of this shift is the increasing realization that the categories of greatest importance to taxonomists are not kingdom, phylum/division, class, order, family, genus, and species (the last term being used here in the older sense of a taxonomic rank) — the important categories are clade and species (the second term now used in the newer sense of a category of biological organization). To the extent that the unified species concept represents the more complete acceptance of this newer view of species, it represents a central component in the future of taxonomy.

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Definitions and Phylogenetic Nomenclature

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Recent developments in biological nomenclature suggest advantages of phylogenetic alternatives to more traditional Linnaean approaches. My aim is to discuss some fundamental aspects underlying biological nomenclature in general and phylogenetic nomenclature in particular. A basic assumption, in both traditional and phylogenetic nomenclature, is that taxon names can and should be defined. From the ontological view of individuality I question this view and argue that taxon names only refer since no defining properties are involved for particular clades. Even if we accept the idea that a taxon is a natural kind with a historical essence, and thus has defining properties, I see problems of definitions from an epistemological and inferential point of view. Our conceptualization of phylogeny is dependent on our hypotheses. Therefore, definitions based on discarded hypotheses are problematic. Instead, each new and accepted hypothesis should form the basis of our conceptualization. Another theme in this paper is what should count as the same taxon under different hypotheses. Can a phylogenetic definition guarantee that a name always refers to the same taxon under different hypotheses? I argue that this is questionable. I conclude by suggesting that we need to rethink the role of definition, sameness, and stability in nomenclature. Rethinking these concepts, I believe, will shed some new light on biological nomenclature. My conclusions strongly favor a phylogenetic approach to nomenclature but also suggest that we, besides some practical problems, still have many interesting theoretical and philosophical aspects to take into account.

Names play a prominent role both in science and life in general. Without names our ability to communicate is severely hampered. From this perspective, biological taxonomy is, perhaps, the most fundamental discipline in the biosciences because it is involved with naming biodiversity and, thus, constrains what biologists in general can talk and will think about. The names themselves function as the common currency in biological thinking. Consequently, taxon names have both a high general scientific interest as well as a more specific value for understanding and describing biodiversity.

Needless to say, biological nomenclature has a long and influential history. Linnaeus was the first to introduce a formalized approach to biological nomenclature during the 18th century with important works like *Species Plantarum* (Linnaeus 1753) and *Systema Naturae* (Linnaeus 1758). The first nomenclatural code, the Strickland Code, was published nearly 100 years later (Strickland et al. 1843), with Darwin as one of the authors, and it has been followed by more specific codes, such as the botanical code (ICBN) and the zoological code (ICZN), that are in use today. Despite many modifications, most modern approaches to biological nomenclature have their roots in the writings of Linnaeus and the notion of taxon names has remained relatively unchanged during the

last 250 years. Obviously, evolution was not in the limelight of biological thinking in the 18th century and a valid question is whether these nomenclatural approaches can be reconciled with phylogenetic theory.

In answer to this question, one can note an increased awareness in the scientific literature during the last 30 years that Linnaean based nomenclature has difficulties in conveying information about phylogeny (e.g., Griffiths 1973, 1974; de Queiroz 1992, 1994, 1997; de Queiroz and Gauthier 1990, 1992; Ereshefsky 2001; Pennisi 2001). A major concern is that the nature of the phylogenetic tree seems to be incompatible with the use of Linnaean ranks (de Queiroz and Gauthier 1990). Consequently, efforts are now underway to make phylogeny the central principle in nomenclature and to develop a rank-free system where names refer directly, and only, to clades without the detour of taxonomic ranks (e.g., de Queiroz and Gauthier 1990, 1992; Bryant 1997; Härlin 1998, 2003a, 2003b; Cantino and de Queiroz 2000; Kluge, in press; see Pleijel and Rouse 2003 for a review).

The aim of the present paper is not to review shortcomings in Linnaean-based systems (e.g., de Queiroz 1997 and Ereshefsky 2001), but instead to highlight some more general issues (e.g., definition, sameness, stability) in nomenclature. Recognizing these issues does not discourage the introduction of a phylogenetic nomenclature. On the contrary, what will emerge from the following discussion is a strong support for making phylogeny the central tenet also in nomenclature.

PHYLOGENETIC NOMENCLATURE

In the early 1990's de Queiroz and Gauthier (1990, 1992, 1994) proposed a method for making phylogeny the central component in biological nomenclature. These papers have received a relatively large amount of attention, both positive (e.g., Sundberg and Pleijel 1994; Schander and Tholleson 1995; Cantino et al. 1997; Ereshefsky 2001; Härlin 1998, 2003a, 2003b; Pleijel and Rouse 2003; Pleijel and Härlin 2004) and negative (e.g., Lidén and Oxelman 1996; Dominguez and Wheeler 1997; Nixon and Carpenter 2000; Benton 2000; Keller et al. 2003). A set of rules aimed at disciplining phylogenetic nomenclature, i.e., the PhyloCode (Cantino and de Queiroz 2000), is now present as a draft version on the web <<http://www.ohiou.edu/phylocode>>. According to de Queiroz (1997), phylogenetic nomenclature is the logical extension of the Darwinian revolution that previously has taken place in the discussions on the ontology of taxa (e.g., Ghiselin 1966, 1974, 1997; Hull 1978; Frost and Kluge 1994) and in the developments of phylogenetic inference that begun with Hennig (1966). This is what O'Hara (1988) calls tree thinking.

A modern, but traditional, system that has its roots in the writings of Linnaeus strives to achieve nomenclatural stability by utilizing types and ranks. Within such a system the name is connected to the type and a particular rank while the circumscription is made in order to demarcate one taxon from another. By tradition, morphological characters have played an important role in circumscriptions. The idea is to somehow maintain stability when adopting a new hypothesis by letting the name refer to the "same" taxon with regard to its content (i.e., terminal taxa and similar morphology) (see also Bryant and Cantino 2002). De Queiroz and Gauthier (1990) instead suggested a rank-free system where the taxon name was attached directly to a clade by a phylogenetic definition (be it node-, stem-, or apomorphy-based) that includes two or more specifiers (Cantino and de Queiroz 2000) but makes no reference to types or taxonomic rank. As a consequence, when adopting a new phylogenetic hypothesis, nomenclatural stability is provided by the phylogenetic definition referring to the same ancestor irrespective of the hypotheses. Phylogeny does, indeed, become the central principle of nomenclature, but is the phylogenetic approach without problems? Let us take a look at some potential issues.

Definitions

The explicit nature of phylogenetic definitions highlights some fundamental problems with any nomenclatural system that attempts to fit historical entities like clades. The problems of definition, sameness, and stability that I will discuss below are thus not restricted to the phylogenetic approach. Any system based on definitions (i.e., also Linnaean-based methods) suffers from similar problems (Härlin 1998; Härlin and Sundberg 1998; see also Moore 1998, 2003; Kluge, in press).

Whether definitions are applicable or not depends on the ontology of taxa. If taxa are considered to be ontological individuals, i.e., spatio-temporally restricted particulars whose existence are due to the contingent nature of evolution, then no defining properties are available (e.g., Ghiselin 1966, 1995, 1997; Härlin 1998; Härlin and Sundberg 1998; Keller et al. 2003; Kluge, in press). Names of individuals are proper and just refer to the referent through an initial ostensive connection (Ghiselin 1997) and a causal chain of reference (Kripke 1980; Evans 1982; Devitt and Sterelny 1999). That is, the name is transmitted, beginning with the ostensive attachment, from sender to receiver through history — history shapes the connection between the name and the named thing. However, from an ontological point of view, taxa need to be natural kinds (e.g., Mahner and Bunge 1997; Griffiths 1999) in order for definitions to be applicable (but see de Queiroz 1992, 1995). Natural kinds, unlike particulars, are unrestricted in time and space and, thus, have defining properties; either as shared organismal features (Mahner and Bunge 1997) or as particular common descents, historical essences in the words of Griffiths (1999). Hence, from a philosophical point of view there seems to be an inconsistency in connecting a definitional approach of nomenclature with the individuality thesis of taxa (Härlin 1998; Härlin and Sundberg 1998; Keller et al. 2003; Kluge, in press). An ontology of taxa as individuals, which seems appropriate in an evolutionary paradigm, requires a purely referential approach to nomenclature (Härlin 1998; Härlin and Sundberg 1998; see below for further discussion). On the other hand, one might argue that a tree-based approach to nomenclature (like above) is applicable irrespective of the ontology of taxa as long as one is aware of the different assumptions and implications involved — the ontology of taxa constrains explanations and predictions (Pleijel and Härlin 2004).

However, setting the ontological issue aside, there are also epistemological problems of definitions when applied in phylogenetic inference. By epistemology I mean the process of phylogenetic inference and the hypotheses that it generates. As biologists interested in phylogeny we try to infer history. Our main problem is that history cannot be directly observed — we have to rely on indirect evidence from extant and fossil specimens. Consequently we are left with hypotheses of history rather than the “real” history. Most efforts in nomenclature, be they Linnaean or phylogenetic, aim at attaching names on reality. For instance, the phylogenetic nomenclature underlying the PhyloCode uses definitions (like “Mammalia” being defined as the least inclusive clade comprising Monotremata and Eutheria) and claims that the common descent of a clade makes taxa sharing that descent logically and necessary parts of that clade (de Queiroz 1992, 1995; but see Ghiselin 1995; Härlin and Sundberg 1998); a natural kind perspective of taxa (e.g., Griffiths 1999) that echoes individuality! Furthermore, the names and definitions primarily refer to real ancestors and not hypotheses. Nevertheless, a definition (like the one of “Mammalia” above) rests on a purely inferential foundation and only makes sense within the context where it was originated (see below). This system, introduced by de Queiroz and Gauthier (1990) and labeled the phylogenetic system of definition (PSD) by Härlin (1998), also suggests that, once a taxon is conceptualized, the definitional approach refers to reality by navigation through possible hypotheses via an autopilot — the initial definition. In other words, phylogenetic definitions of taxon names suggest (1) involvement

of logical and necessary properties; (2) that a definition is erected once — no redefinitions allowed; (3) that the definition determine the inclusiveness of a taxon name in each successive hypothesis; and (4) that sameness is achieved through reference to the same real ancestor/ancestry across hypotheses.

However, at the interface between real history and observation we have the hypotheses of evolutionary history. And, these hypotheses form our conceptualization of history. Consider the example in Figure 1. Observations on extant specimens have led to a hypothesis of five different species (A, B, C, D, and E). Based on a phylogenetic analysis

we have reached a hypothesis of their phylogenetic relationships as depicted in the right hand tree. This tree structure, in turn, leads us to attach a name *alpha* to the ABC clade. The tree structure, the hypothesis of evolutionary history, thus, provides us with a particular conceptualization of history that we for some reason find important enough to name. According to the PSD approach we also attach a phylogenetic definition to the name. Such a definition could take the form “the least inclusive clade comprising A and C” and involves a subjective choice of specifiers like A and C. Again, the tree structure is most likely also to determine the choice of specifiers. Two important points should be made here. First, to what history the name refers may (is likely to) differ between hypothesis (right hand tree) and reality (left hand tree). Reality will always be cast in the shadow, somehow as in Plato’s cave metaphor. Accordingly, there will often be a discrepancy between what history the name refers to within a hypothesis and what history it may refer to in reality — a discrepancy over which we do not have any control. In other words, a name (and its definition) may imply different histories in hypotheses and reality. The impossibility to ascertain the true evolutionary history suggests that it might be beneficial to attach names to phylogenetic hypotheses only. After all, hypotheses provide us with our conceptualization of history and play the leading role in all parts of biology (Fig.2). Second, the subjective choice of specifiers plays a decisive role in the interpretation of taxon names under revised phylogenetic hypotheses (Fig. 3). That is, the choice of specifiers shapes our conceptualization of reality — it determines what we will think and talk about (Figs. 2 and 3). Inasmuch as a strict definition-

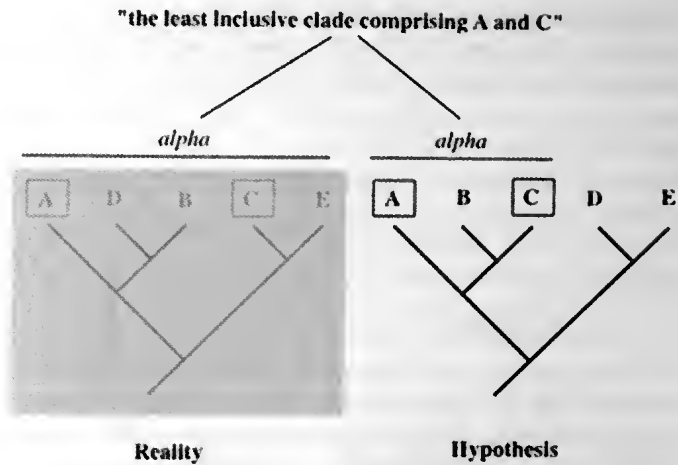


FIGURE 1. The phylogenetic hypothesis (right hand tree) provides the impetus for naming. It also forms the basis for picking specifiers and designing phylogenetic definitions. It is likely that that a taxon name refers differently in reality (left hand tree). This incongruence is out of our control and a reason why names and reference are better restricted to hypotheses only. Specifiers are marked with squares.

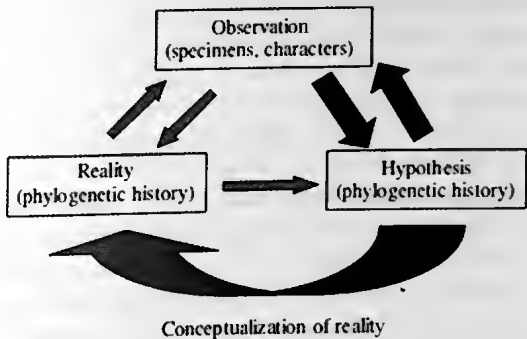


FIGURE 2. Flow diagram illustrating the central role played by the phylogenetic hypothesis and how it conceptualizes our view of phylogenetic reality.

al approach, like the PSD, does not allow for modifications in reference and/or choice of specifiers when a new hypothesis is preferred it leans heavily on the initial and subjective choice of specifiers and type of definition. It seems as if subjectivity is introduced, but not nursed.

Sameness

Connected to the issue of definition is the problem of sameness and stability. What should count as the same taxon under two successive hypotheses? In the Linnaean-based methods, nomenclatural stability equals sameness of content, and this goal is tentatively obtained by means of type and rank association. The PSD aims at another sameness, in the sense that a taxon name always refers to the same ancestor and that the phylogenetic definition with its specifiers is the tool to be used to achieve this sameness/stability. De Queiroz (1997) has clearly demonstrated that rank based systems, like the Linnaean one,

suffers from instability in both name and taxon content. Similarly, sameness problems of the name “Mammalia” have been highlighted by Rowe and Gauthier (1992). My point here, however, is that phylogenetic definitions do not necessarily solve problems of sameness. As hinted in the previous lines, there are many possible kinds of sameness. Content in terms of terminal taxa (and/or internal lineages), ancestor (as in a particular point in history), and ancestry (as in the entire relational history of a clade) are all possible candidates for a concept of sameness (Härlin 1998; 2003b). Bryant and Cantino (2002) suggested that proponents of traditional nomenclature tend to emphasize the importance of taxonomic content while proponents of a PSD emphasize the importance of reference to the same ancestor. In a sense this is true, but it represents an oversimplified view of evolutionary history (Härlin 2003b) because all of these aspects are tightly intertwined and, thus, not easily, or perhaps not even possible, to separate. Strictly focusing on content is unfortunate as this restricts terminal taxa to atemporal entities, which these are not. Strictly focusing on ancestors is equally unfortunate since terminal taxa are their ancestors and vice versa (Lidén 1990), i.e., terminals are their ancestors albeit at a later point in time. Focusing on the entire ancestry of a clade puts the relational history of lineages (both terminal and internal) in focus, which is a very strict view of sameness. Arguing for sameness in terms of content is an ahistoric approach. Arguing for

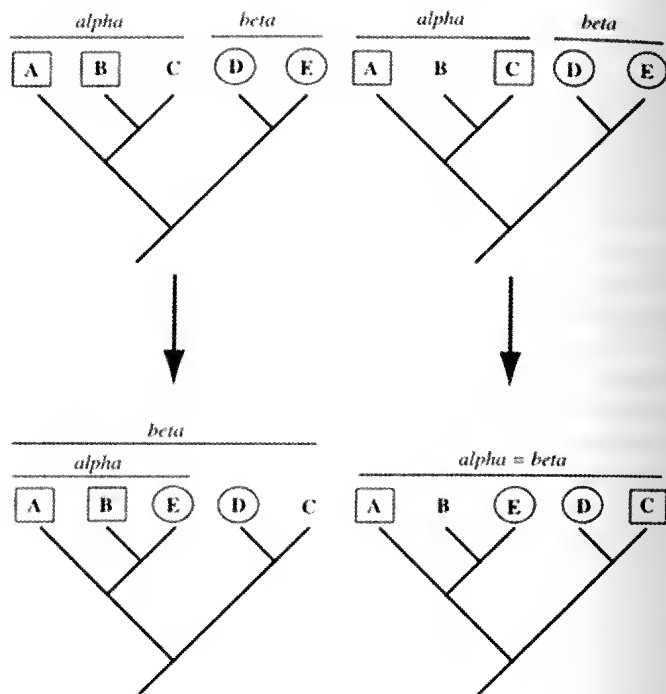


FIGURE 3. Within a definitional approach to nomenclature the acceptance of a new hypothesis comes with an automatic shift in reference. The choice of specifiers plays a crucial role in this process. Different specifiers, different reference in forthcoming hypotheses. The subjective choice of specifiers dictates our future conceptualization of reality. Specifiers for *alpha* are marked with a square and specifiers for *beta* are marked with a circle. In the left-hand trees the name *alpha* is defined as “the least inclusive clade comprising A and B,” whereas in the right-hand trees as “the least inclusive clade comprising A and C”. The name *beta* is defined as “the least inclusive clade comprising D and E” in both left and right-hand trees.

sameness in terms of ancestor without taking terminal taxa into account is an equally ahistoric approach. Arguing for sameness in terms of ancestry is a historic but too strict approach to sameness. My conclusion is that we need to loosen up the definitional approach and rethink the need for sameness on a case-by-case basis.

RELAXING THE DEFINITIONAL APPROACH

Arguably, the phylogenetic approach to biological nomenclature initially sketched by de Queiroz and Gauthier (1990) carries a lot of promise with it — not the least by making evolutionary history its very foundation. Still, as we have seen above it also carries some historical burden in terms of definition and the need for sameness. An effort to loosen up both the role of definition and the need for sameness across hypotheses is the phylogenetic system of reference — PSR (Härlin 1998, 1999; see also Kluge, *in press*). The core features of a PSR are (1) to avoid definitions since it is argued that no logical and necessary properties are involved (i.e., a particular common descent is not a defining property — taxa are individuals, not natural kinds); (2) to primarily refer to phylogenetic hypotheses; and (3) to force us to reconsider reference and specifiers with each new and accepted hypothesis.

In practice, a PSR is as phylogenetic as PSD since both aim at directly attaching names on clades. However, while a PSD has its roots in a legislative approach to nomenclature a PSR is closer to ordinary language and how names and reference evolve. The need to modify the link between the name and the named thing is common in language (Evans 1973, 1982) and also illustrates that nomenclature is meant to allow messages to be exchanged between senders and receivers. A dialogue evolves which means that an initial definition may not be enough for future communication. Forcing the taxonomist to reconsider reference and specifiers of a taxon name with each new and accepted hypothesis shifts the focus from a hidden reality to an explicit hypothesis about it. Reconsidering specifiers and reference with each new and accepted hypothesis also allows for a reinterpretation of what we mean by the same taxon. It is possible to take content, ancestor, as well as ancestry into account and to make a subjective choice of how the association between the name and the named thing should be re-established (including the possibility to change the name). Admittedly, this increases the level of subjectivity. However, once subjectivity is introduced it must be nursed in order to maintain effective communication between sender and receiver.

A phylogenetic system of reference combines the best of the Linnaean systems with the best of the PhyloCode (PSD). With the PhyloCode it shares features like being rank-free, explicitly phylogenetic, and the possibility to name parts of a tree without affecting other parts of the tree. On the other hand it allows for new circumscriptions, modifications in reference and choice of specifiers as does the Linnaean methods within their particular framework.

CONCLUSIONS AND DIRECTIONS FOR THE FUTURE

Phylogenetic nomenclature is likely here to stay. Exactly in what form is still to be settled. Any system intended for the future needs to get rid of ranks. Ranks are incompatible with phylogeny (Griffiths 1974; de Queiroz and Gauthier 1990) and also invite illegitimate, and in some areas widespread, comparisons between taxa of the “same” rank (Mishler 1999; Minelli 2000). Both PSD and PSR fulfill this requirement. These methods allow for a nomenclatural system of hierarchic and nested uninomials (or rather multinomials) that better fits a rank-free system (Härlin and Härlin 2001). A system for the future should not rest on the necessity of stability. Stability in either/or both names and content is a utopia that does not fit an evolutionary and scientific world-

view. Both names and reference should be allowed to change. That is, taxon names need not be unique — only traceable. Traceability and unequivocal communication should be the prime goals of nomenclature, not stability.

As I see it, a future system of nomenclature needs to combine the freedom of traditional Linnaean-based methods with the explicit phylogenetic operationality of the PhyloCode approach. Such a system will take nomenclature to a new dimension with a focus on hypotheses and disruptiveness without losing traceability.

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Publications in Taxonomy as Scientific Papers and Legal Documents

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Taxonomic papers are unique, in the world of scientific literature, because of their double status. In so far as these papers include descriptions of new taxa or other nomenclatural acts, they are not just scientific publications, but also legal documents. From the latter point of view, their value lasts forever, under the current Codes of Nomenclature. This is primarily due to the Principle of Priority, the single most important principle acknowledged by taxonomists when addressing nomenclatural conflicts due to homonymy or synonymy. Problems due to the burden of the old literature are worsened by the difficulty of accessing many old items and by the plurality of languages in which this literature is written. This is at the same time cause and effect of the low average profile of taxonomic literature as measured in terms of impact factor. Because of this odd marriage of scientific merit and legal significance in taxonomic papers, these are not subject to the Darwinian competition ruling over papers in other disciplines. A move towards uncoupling scientific content and legal value of taxonomic papers by adopting an efficient registration system of new names and nomenclatural acts would not simply help taxonomists in their daily work but also considerably raise the standard profile of their published work.

These are exciting but also critical times for taxonomy, man's oldest profession (Hedgpeth 1961). Happy times, on the surface. Major scientific journals like *Science* and *Nature* frequently feature commentary papers stressing the importance of the discipline, as a key tool to obtain a better grasp of the biosphere's whole biological diversity (e.g., Blackmore 2002). But the same papers also point to the impossibility for taxonomy to go ahead effectively so long as it is forced to rely on the current modest budgetary resources and decreasing human capital. To be sure, this is the single worst problem for taxonomy, but hardly one that can be effectively solved without a serious effort to make the public image of taxonomy to match the enormous scientific and social value of its century-old output.

Several papers (e.g., Gee 2000; Bisby et al. 2002; Godfray 2002a, 2002b) have stressed the need for taxonomy (especially animal taxonomy) to embark on an information revolution as the only possible way to make existing taxonomic knowledge immediately accessible, to substantially improve the current pace of species description and to be eventually acknowledged as big science, on a footing comparable to that of genomics, neurosciences, or space research.

I will not add more wood to this fire. Instead, I will focus attention on a well-entrenched set of sociological problems, whose consequences have been very heavy on the procedures by which taxonomists communicate among themselves, and with the remaining scientific community. In my opinion, the inadequate way taxonomists communicate the results of their research is impairing

their output to an increasingly damaging level. Adequate measures aiming to change this state of affairs can, and must, be rapidly enforced.

THE NATURE OF TAXONOMIC LITERATURE

Is a taxonomic paper like an average scientific paper? Yes and no.

It is, in so far as it describes selected features of the natural (biological) world, in a more or less formalized language, and according to generally agreed comparative schemes.

On the other hand, taxonomic literature differs from the equivalent product of other sciences' efforts in several important respects.

First, taxonomic literature is not written in a single, common language. Recommendation 13B of the International Code of Zoological Nomenclature (ICZN) states that "Authors should publish diagnoses of new taxa in languages widely used internationally in zoology. The diagnoses should also be given in languages used in the regions relevant to the taxa diagnosed." This means that if I describe a new centipede species from Southeast Asia in my mother language (Italian), which is still fairly widely used internationally in zoology, I should perhaps add a diagnose in Vietnamese. Is this right the way science advances in disciplines other than taxonomy?

Why is there no common language in our papers? Why have taxonomists failed until now to adopt English universally? (cf. McNeill 1997) The Bacteriological Code has tackled this problem and all species descriptions in this area are now expected to be in English, but things are different in zoology.

To be sure, the suggestion to abandon all other languages once and forever, in taxonomic papers, has been floated in the recent past, when drafts were circulated of what eventually became the current fourth edition of the ICZN, published in 1999 and in force since January 1, 2000. The ado of the opposing comments and the wild diversity of alternative solutions proposed at that time were such as to invite the International Commission on Zoological Nomenclature to refrain, for the time being, from putting into the Code an Article enforcing English as the universal language of taxonomy. Were the same question discussed today, however, the chances would be much higher that such a decision would be eventually adopted. One may wonder from where such objections to English as the universal language of animal taxonomy were actually raised. As expected, the strongest voices came from those European countries whose national languages have a long history of use in taxonomic literature. Less expected, however, is the fact that this reaction involved professionals and amateurs alike. This fact, however, opens an important perspective on the sociology of taxonomy. This is, indeed, a field in which, even today, at the beginning of the third millennium, there is still an active and most welcomed input from non-professionals. I shall return to this point again.

But let's go back to the original question, whether or not taxonomic literature has the same nature as the printed output of the other scientific disciplines.

Besides the difference due to the lack of adoption of a single international language, there is another unusual circumstance that, again, impairs the spread of taxonomic information. Ironically, this problem derives from the very adoption of provisions originally devised to give taxonomy rules for making internal and external communication more easy and straightforward. Nomenclature is ruled by international codes: for animals (International Code of Zoological Nomenclature, ICZN), plants (International Code of Botanical Nomenclature), and prokaryotes (International Code of Nomenclature of Bacteria), whose declared aim is to promote the universal-ity (and stability) of the scientific names of organisms.

This means, for example, that there are internationally agreed principles according to which

we can decide which of two synonyms has to be used, or which of two homonymous species may retain the name they have inappropriately shared for a while. These rules, and the many other and sometimes cumbersome ones contained in the Codes, are certainly useful. Necessary, indeed, but the very existence of codes to which zoological or botanical nomenclature should adhere has a generally ignored consequence. All taxonomic papers, in so far as they include the description and naming of a new taxon, or any other act of nomenclatural relevance, are something more than ordinary pieces of scientific information. In so far as they cope with the requirements of the codes, they are also a kind of legal documents. The ICZN, for instance, fixes a series of criteria to be met (Articles 7-9) for a publication to be regarded as published for the purposes of zoological nomenclature, and other criteria (Articles 10-20) for determining the availability of published names or nomenclatural acts, while two more articles (Articles 21-22) specify how the publication date has to be determined, something of fundamental importance for the application of the Principle of Priority, the veritable keystone of the whole system.

All this is good, in principle. The codes provide rules for getting nomenclature as straight and stable as we need to have. But we are paying an exorbitant price for that. If a taxonomic paper containing a little bit of nomenclatural information is a legal document, we must keep it forever. And to read through it, whenever we think that a new name or another nomenclatural act it might contain should be compared, in the light of the code, with other names or acts that possibly interfere with the name(s) of the taxon with which we are concerned. Partial and well-qualified limitations to the Principle of Priority, such as those embodied in Article 23 of the current edition of the ICZN, hardly lower this burden. To legitimate the use of a name in prevailing use without the need to apply to the International Commission for a special ruling, a taxonomist has to state that the senior forgotten synonym has never been used as a valid name since 1899, whereas its junior synonym has been used for that species in at least 25 different works by at least ten authors in the immediately preceding fifty years and for a time span of not less than ten years. Let's imagine how extensive bibliographic research through our "legal papers" this may require.

WHY DID TAXONOMIC LITERATURE DEVELOP THIS WAY?

In an ideal world, one could imagine that the scientific nomenclature of organisms could move towards a very simple set of internationally agreed upon rules and the simultaneous establishment of a central office where all new names are immediately registered as soon as they are proposed. Still better would be a system where new names take existence from the time they are registered and simultaneously made available, on line and for free, to all interested users. One may wonder whether a real, adequately staffed registration office would be actually required. In principle, registration could be, or become, automatic. A taxonomist ready to add a new entry to the official record of existing animal names would find, at the official registration website, a suitably arranged input form, with compulsory fields corresponding to all Code's requirements for name availability. At the same time, automatic check of the proposed new entry against the names already in store would prevent primary homonymy, including cross-kingdom identity of genus names. Such an automatic procedure could be probably set up following a reasonable time of trial with assisted registration and optimization of the input form.

The relationship between the registration of a new name and publication of the taxonomic paper connected to it would be similar to the relationship between placing a new protein or nucleotide sequence in one of the internationally recognized molecular databases and publishing a paper where the molecule is discussed in terms of structure, or exploited for its phylogenetic significance.

In such an ideal world, the use of names would not necessarily require reading, or citing, the taxonomic papers. In many cases, referring to the data in storage at the web-based registration database would cover all needs of documentation. Reading and citing papers, of course, would still be needed for additional, critical information. The point to be emphasized is that a first-rate taxonomic paper would continue to be read and cited, whereas poor papers would reasonably fall into irretrievable oblivion. Not surprisingly, this holds true today for papers in nearly all biological disciplines other than taxonomy.

Taxonomy's real world, however, is very different from that ideal condition. It is a world where bad old papers may have a high chance of being cited (even if, perhaps, not read) only because of the names first proposed there, that is, because of their legal value, as opposed to their intrinsic scientific value.

We have internationally accepted rules of nomenclature, but these rules were established *post factum*, that is, at a time zoologists and botanists already had to cope with a few million names, originally proposed outside any agreed set of rules. This is while the basic philosophy behind the zoological (and botanical) code is still one of "let's do our best with what we have inherited from the past", rather than "let's set up the most efficient structure for the present and the future."

The only major effort towards a rational management of scientific names of organisms has been accomplished by bacteriologists. Until 1979, the Bacteriological Code operated in a way similar to the Botanical Code, from which it was derived. Originally cared for under the Botanical Code, the initiative to start a Bacteriological Code took form in the 1930s, with the first draft Code being produced by 1939. The first published version was issued in 1948, with revisions being published in 1958 and 1966. The radical break with the past came with the 1976 revision which was re-worded, simplified, where possible, and the concept of the "valid publication of a name" (i.e., registration/official indexing) was introduced. It is this system which was the model for the BioCode and has, in turn, influenced the PhyloCode. The new starting date is January 1, 1980, but care has been taken to retain reference to the older names, authors and literature which should be carried forward into the future. From that date, all new names or nomenclatural acts take effect following their "registration" publicized through one of two systems via one journal, the *International Journal of Systematic and Evolutionary Microbiology* (formerly, *International Journal of Systematic Bacteriology*). In one system, original publications in the journal may be used as the vehicle of registration, providing the rules of the Bacteriological Code are followed, and in the other, names published outside the journal may be entered in a list, which gives them the status of being registered. This is, indeed, something that is fairly close to the ideal world I have just sketched. But this may be describing an ideal world, one that is, unfortunately, still very far from today's zoological and botanical nomenclature. To be sure, repeated efforts have been made, for animals and plants alike, to update the codes in the same sense as bacteriologists did. No workable solution, however, has been found until now, for a complex and ill-defined mixture of technical and political problems: *Technical* — to produce a list of all existing names is certainly not a problem of data base management, but one of critical data mining in an already enormous literature; *Political* — Some people fear that registration might, in fact, become a kind of censorship that would limit the current extensive freedom taxonomists enjoy in writing their papers. Censorship, however, should occur at the peer review stage, if necessary, not on registration. All names meeting the requirements of the Code must be acceptable for registration without any other argument.

TAXONOMISTS, POOR BUT PROUD

The impact factor of the journals in which you publish your papers is often used as the most

reliable proxy of your scientific status by panels empowered to assign research grants and even to decide on appointments and promotions. This is a serious drawback for taxonomists, as the access to the highest impact factor journals is forbidden even to the best papers they may produce (Krell 2002), with the exception, perhaps, of the first description of some new fossil hominid or feathered dinosaur. If we take as the reference point the journal ranking provided by the *Journal of Citation Report* for 2001, the highest ranking zoological journals (in term of impact factor) where you may possibly publish the description of some new taxa are probably (Minelli 2003) *Zoologica Scripta* (rank 6), *The Journal of Mammalogy* (rank 12) and *The Zoological Journal of the Linnean Society* (rank 22). The same is true, if not worse, for entomology (*Systematic Entomology*, rank 6; *Annals of the Entomological Society of America*, rank 22; *Entomologica Scandinavica*, rank 28) or for botany (*Annals of the Missouri Botanic Garden*, rank 13; *American Journal of Botany*, rank 17; *Systematic Botany*, rank 22).

On the other hand, the taxonomist can always look forward to a unique long-term reward. Owing to their status as legal documents, taxonomic papers last virtually forever. Linnaeus and his followers are the true immortals of scientific literature. It is perhaps a pleasant feeling, to think that somebody will probably need to look into the slimmest of your papers in one or two centuries from now, whereas the overwhelming majority of papers in chemistry or physics, but also in experimental biology, definitely will be buried within a short time. How large, however, is the cost of this personal ambition in terms of efficiency in communication and intellectual progress?

CHANGING THE RULES

Inevitably, we must change the rules, without further delay. We need fast, efficient and exhaustive access to everything which matters in science, and freedom from never-ending bibliographic searches on scientifically uninteresting papers.

To be sure, these needs are shared by all scientists, in all scientific disciplines. The problem is, that taxonomists have some practical problems peculiar to them, and these problems must be quickly and adequately solved by getting rid of persisting old-fashion procedures, nevertheless paying due attention to the peculiarities of this discipline. A critical reading of the current codes of nomenclature will provide useful insights. For example, why are taxonomists uniquely concerned with the durability of the media in which their data are published, that is either ink on paper, or some of the modern electronic supports? Why is this concern not shared by other scientists? What every taxonomist wants is correct bibliographic information acknowledging priority, but pure temporal priority should not overcome scientific merit. As a former President of the International Commission on Zoological Nomenclature once put it, is it more important to serve the living or to respect the dead? (Ride 1991).

A PROPOSAL

I firmly believe that taxonomy will make a very long leap ahead if provisions are taken soon for uncoupling the scientific from the legal aspects of taxonomic papers (Minelli 2003). All kinds of information relevant to the application of the Principle of Priority, and the other rules of the Codes which are intended to promote stability and universality of scientific nomenclature, should be stored in a public, freely accessible, and durable database. That is, all legal aspects deriving from the proposal of a new name, or other nomenclatural act, should not be linked to the publication of the paper in a conventional journal, or on the web, but the relevant information should be deposited in this internationally recognized database. The procedure would be similar to depositing a new

nucleotidic or aminoacidic sequence in one of the major molecular data banks, to accompany a paper where this sequence is analyzed and discussed. In the case of names, however, entering the data in the official database would be much more than a condition to be discharged before the paper goes eventually to the press, or to the website, because of the legal implications deriving from the existence of the international codes of nomenclature with which scientific names must comply.

On the other hand, taxonomic papers would enjoy, at last, the same fate of all other scientific papers. As publications in the Darwinian world of scientific literature, they will continue to be read and cited according to their intrinsic value, thus contributing in a less biased way to raise or lower the impact factor of the journals where they will be published. We can expect that in the long run, higher-profile, higher-impact factor journals will increasingly host high-quality taxonomic papers.

Thus, adopting these new procedures would doubly benefit our research. First, and immediately, by providing a much more effective and less time-consuming use of the literature. Second, over a longer time span, by raising the status of taxonomy and taxonomists and, thus, the chances of getting better footing in many research institutions.

Enforcing the measures I am suggesting here means, basically, to establish an effective system for the registration of names and nomenclatural acts. As mentioned before, bacteriologists have already adopted these kinds of procedures and their example will provide useful advice to zoologists and botanists. To be sure, the much larger number of animal and plant names still in existence, compared to those with which bacteriologists currently have to deal with, will require much more expensive and more articulated solutions. Expensive, however, does not mean impossible. To name just two recent successful exercises, recall that with a four-year effort a team of 272 zoologists managed to produce a list of the more than 55,000 animal species recorded for Italy (*cf.* <http://www.faunaitalia.it/checklist/>), a result that provided impetus for the more ambitious project of listing — with the added bonus of distribution data by country — all animal species of Europe, a project completed in late 2004 (*cf.* <http://www.faunaeur.org>).

Any registration system will necessarily have two components: a thesaurus of existing names (at the starting date of the new regime) and a procedure for the validation of the new names, according to a suitable protocol.

A first task would be thus to mine the literature for legally relevant information. Retrieving the legally relevant information contained in the taxonomic literature is a far from trivial job; it requires adequate professional skills.

Storing all legally relevant nomenclatural information in a public database will have important consequences for other aspects of taxonomic practice. For example, it seems sensible to suggest that all type specimens, which are the material vouchers of species names, should belong to public collections. One could object that many private collections are better curated than many public collections are, but things may change if an international effort were to be made to ensure a suitable location for these precious materials. To be sure, there might be serious problems with the existing type specimens which belong to private collections. Provisions to move them to public collections may find strong resistance that could translate into an enormous increase of their market value.

On the other hand, I do not think that the new measures I am suggesting, in particular the requirement for type specimens to be put in public collections, would cause major troubles in that precious workforce of amateur taxonomists which is still so strong in several European countries and especially active in entomology and malacology. Cooperation between professionals and amateurs is often excellent. For example, public collections host nearly all the types of the taxa described by one of the most prolific descriptors of our times, the Italian amateur entomologist Roberto Pace, the author — until June 2003 — of 3472 insect species (mostly, aleocharine rove beetles). And in malacology, Bouchet (1997) documented that amateurs currently contribute some

28% of the new species descriptions, whereas only less than 1% of the corresponding types are kept in private collections.

WILL IT BE EASY TO CHANGE?

Summing up, I think that taxonomists face the opportunity of improving dramatically both their status and the quality and quantity of their output if they are ready to establish effective measures for uncoupling the legal aspects from the scientific content of their publications. This will require a few changes in the Codes, but this is far from being the most difficult problem. At the core of the change there must be a true revolution in the attitudes of taxonomists towards their work and the work of their peers. Taxonomists must become aware that their work is a part of the human collective endeavor to obtain a better knowledge of the world. In this endeavor, the intrinsic value of one researcher's contribution, thus, will be multiplied by the links he or she develops to the works of others, and even if, over a shorter or longer time span, the original papers are not cited anymore, their contents will be found, improved and reworked, in papers of their successors.

The key question to be addressed by taxonomists is not so much how to best exploit the potentiality of the Web, but how to overcome the cumulative burdens of taxonomic tradition, individuality, the resistance to adopt a common language, and the odd two-sided status of the taxonomic literature.

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